Biotic recovery of conodonts following the end-Ordovician mass extinction

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Biotic Recovery of Conodonts following the End-Ordovician Mass Extinction

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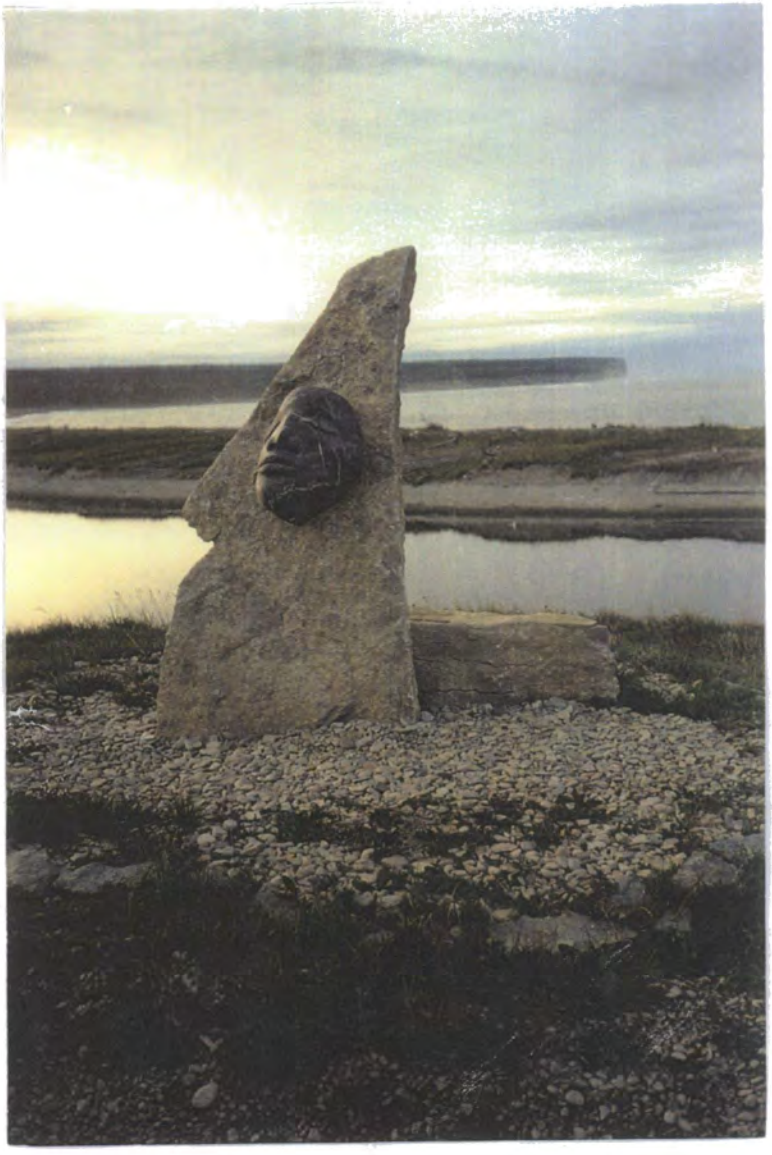

FRONTISPIECE

Sculpture at the mouth of Rivière aux Saumons, Anticosti Island, Québec.
N.B. The base of the Sculpture is a slab of the Oncolite Platform Bed (Laframboise Member, Ellis Bay Formation)

No part of this thesis has been previously submitted for a degree in this or any other university. The work described in this thesis is entirely that of the author, except where reference is made to previous published or unpublished work.

Abstract

The end-Ordovician mass extinction dramatically altered the course of conodont evolution. This extinction event is probably unique in that it can be strongly correlated with a glacial climatic control. This study has identified, through the application of high-resolution stratigraphy, events within the extinction and recovery intervals.

Elements of the uppermost Ordovician Shelf-edge Biofacies were severely affected by the oceanic cooling and introduction of cold-water currents associated with the initiation of the glacial maximum. In contrast, elements of the Shelf Biofacies were more severely affected by the intense cooling, shallowing and overcrowding during the glacial maximum. A number of the Shelf-edge taxa that had survived the glacial maximum suffered extinction at the hands of increasing water temperatures, rising anoxia and/or the cessation of oceanic circulation during the post-glacial transgression.

Recovery was initiated by the appearance of Crisis Progenitor Taxa within the glacial maximum in the Shelf Biofacies and during the post-glacial transgression in the Shelf- edge–Slope biofacies. The Shelf-edge Biofacies identified within the uppermost Ordovician is not recognised in the Lower Silurian. Two main biofacies occurred on the Shelf and Slope, which had directly evolved from their Upper Ordovician equivalents.

The long-term recovery involved the evolution of Crisis Progenitor Taxa and Ecological Generalists within the Shelf and Slope Biofacies (autochthonous taxa). Punctuated equilibrium likely predominated in the Shelf Biofacies as a consequence of widely fluctuating physical conditions. In contrast, the more stable environments of the slope encouraged gradualistic evolution within the Slope Biofacies (*Plus ça change* Model).

Transgressive episodes within the Llandovery, possibly linked to eccentricity cycles, caused the iterative appearance of Long-term Refugia Taxa (allochthonous taxa), sourced from a Pterospathodontid Biofacies. The transgressive episodes also drove elements of the Slope Biofacies onto the shelf.

It has been observed that the mechanisms driving extinction, namely environmental disruption and temperature changes, were also responsible for fuelling the subsequent recovery.

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Introduction

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Introduction

1.1 Introduction

Biotic recovery following mass extinction is an area of research in its infancy. Workers have focused on high-resolution interdisciplinary studies of key localities that span mass extinction boundaries, and the development of standard terminology and testable recovery models (Kauffman & Harries, 1996).

Numerous studies have discussed the distribution of conodonts throughout the Upper Ordovician and Lower Silurian but few have focused on identifying patterns of extinction and recovery through this time interval. The end-Ordovician mass extinction event is unusual in that little controversy surrounds the identification of its causal mechanism. A firm link between the mass extinction event and glaciation has been established. Conodonts ranged from the Cambrian to the Triassic and were affected by a number of extinction events, the end-Ordovician event being one of the most striking of these faunal turnovers (Aldridge, 1988; Barnes & Bergström, 1988).

This study analyses the pattern of conodont extinction and subsequent recovery through the Late Ordovician to Early Silurian. Conodont species from three Laurentian sections, of varying palaeogeographic setting, have been studied and identified systematically. Events within the extinction, initial recovery and long-term recovery intervals have been identified and considered in the light of climatic changes occurring within this period. This has led to the determination of the driving force of extinction and recovery.

1.1.1 Thesis Aims

- To develop a framework including biostratigraphical, chemostratigraphical and sea-level data from the Upper Ordovician to Lower Silurian.

- To study systematically conodont species from the Upper Ordovician and Lower Silurian recovered herein.

- To identify the pattern of conodont extinction, which is crucial to the understanding of recovery.

- To identify the pattern of conodont recovery in the Upper Ordovician to Lower Silurian.

- To determine the causal mechanism of recovery.

1.1.2 Thesis Outline

Chapter 1 introduces the study of mass extinction and recovery. A brief introduction to the palaeobiology of conodonts and the end-Ordovician mass extinction event is given.

Chapter 2 reviews methods of correlating Upper Ordovician to Lower Silurian strata, including biostratigraphy, chemostratigraphy and sea-level cyclicity, which led to the development of a standard framework.

Chapter 3 introduces the biostratigraphy, chemostratigraphy and sea-level cyclicity of the Upper Ordovician to Lower Silurian sections at Lake Timiskaming (Ontario), Anticosti Island (Québec) and Prongs Creek (Yukon Territories).

Chapter 4 discusses the pattern of conodont extinction through the Upper Ordovician and lowermost Silurian in the sections studied herein and in supplementary sections from the literature. The spatial variations in extinction are identified and causal mechanisms for the extinction suggested.

Chapter 5 discusses the patterns and processes operating during the initial and long-term recovery of conodonts following the end-Ordovician mass extinction event. The conclusions of this thesis are presented in Chapter 6. Abbreviated systematic descriptions of the conodonts recovered during this study are given in Appendix A.

1.2 Extinction

Most species that ever lived are now extinct. Extinction can result from the continuous competition between species for resources (background extinction) or, during relatively short intervals of geological time, when a significant percentage of the global biota succumbed to extinction (an extinction event) as the result of a specific event or series of events. There have been five major mass extinction events in the Phanerozoic: Late Ordovician, Late Devonian, Late Permian, Late Triassic and Late Cretaceous (Raup & Sepkoski, 1982; Figure 1.1). Although the existence of mass extinction events was suggested in the early nineteenth century, it remained 'a highly speculative backwater of mainstream palaeontology for most of this century' (MacLeod, 1996, p. 86). The suggestion by Alvarez *et al.* (1980) that a meteorite impact caused the K/T mass extinction event sparked renewed interest in the study of the causes and patterns of extinction. The academic and public interest in the study of mass extinction is reflected in the large number of textbooks (e.g. Stanley, 1987; Albritton, 1989; Hallam & Wignall, 1997) and popular science books devoted to the subject (e.g. Allaby & Lovelock, 1985; Eldridge 1991; Leakey & Lewin 1995). The nature of mass extinction events has become 'one of the most lively and contentious issues in the whole of science' (Hallam & Wignall, 1997, p. 1).

Research in general has concentrated on the identification of possible extinction mechanisms by utilising the sedimentological and geochemical record during periods of faunal extinction. Causal mechanisms fall into two main categories: terrestrial (e.g. sea-level change, climate change, volcanism) or extraterrestrial (e.g. meteorite impact, comet showers; for a discussion see Hallam, 1990; Jablonski, 1990).

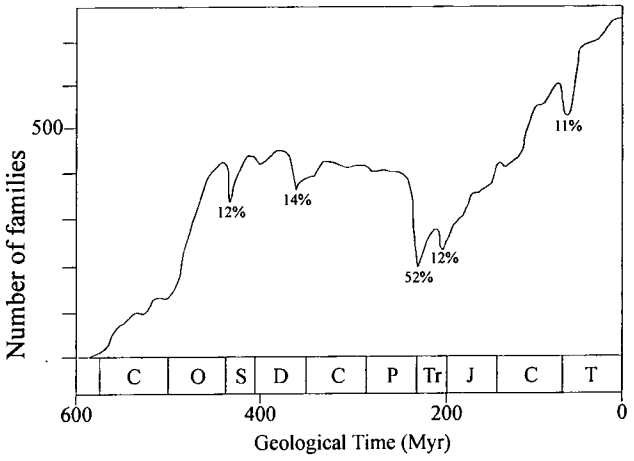


Figure 1.1 The number of families through geological time. From Raup & Sepkoski (1982).

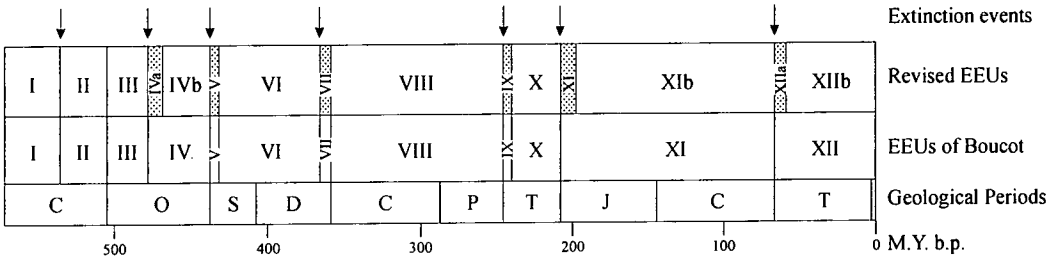


Figure 1.2 Ecological Evolutionary Units (E.E.U.s) of Boucot (1983) and Sheehan (1991). The shaded areas represent reorganisational E.E.U.s, which follow mass extinction events (marked by arrows).

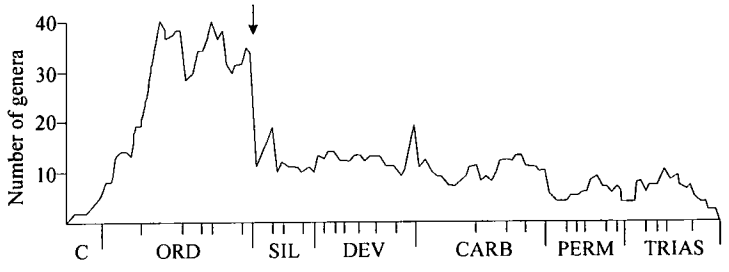


Figure 1.3 The generic diversity of conodonts through their stratigraphical range. The end-Ordovician mass extinction event is marked by an arrow. After Aldridge (1988).

Causal mechanisms are generally thought to vary between extinction events. However, a common and cyclical causal mechanism has been suggested for extinction events over the past 250 million years, following the observation by Raup & Sepkoski (1984) that extinction events during that period occurred every 26 million years. This theory has fuelled an ongoing debate regarding its possible causal mechanisms (e.g. Hallam, 1984; Sepskoski, 1990). A consensus has not yet been reached.

Although a causal mechanism for extinction can be suggested from sedimentological and geochemical analysis, study of the timing and selectivity of faunal extinction must be undertaken if a strong causal link is to be made (e.g. MacLeod, 1996). The pattern of faunal extinction, which may be gradual, stepwise or catastrophic, can help to identify the causal mechanism. A gradual pattern would have resulted from a gradual change in climate, such as sea level or temperature change, whereas a stepwise pattern would result from a succession of events, such as multiple cometary impacts (e.g. Hut *et al.*, 1987). A catastrophic pattern indicates a single, rapid event, such as the impact of a large meteorite (e.g. Alvarez *et al.*, 1980). High-resolution sampling is essential if gradual, stepwise or catastrophic patterns are to be distinguished in the fossil record. The observed pattern of dinosaur extinctions in the latest Cretaceous changed from gradual to catastrophic following detailed sampling of the latest Cretaceous sediments in Montana and North Dakota (Sheehan *et al.*, 1991).

The selectivity of extinction can also help to identify the causal mechanism (e.g. MacLeod, 1996). An example of selectivity widely quoted in the literature is that tropical ecosystems were more prone to extinction than higher-latitude ecosystems (e.g. Kauffman & Harries, 1996; Skelton, 1993). However, Hallam & Wignall (1997, p.18) argued that this effect has 'rarely been quantitatively demonstrated' and that extinction may appear to be more severe within the tropics merely owing to higher initial diversity.

High-resolution sampling may still not give an accurate extinction pattern though, as the true pattern may be distorted by hiatuses in the stratigraphic record, variation in sedimentation rate (e.g. a slow sedimentation rate would concentrate last appearances; Holland, 1995), failure to recognise 'Lazarus taxa', or the backward smearing of the extinction event (Signor-Lipps Effect). Backward smearing results from the fact that

the last true representative of a species is unlikely to have been preserved in the fossil record (Signor & Lipps, 1982). Species whose ranges may be affected by this include species susceptible to syndepositional or postdepositional diagenesis, species whose abundance was low or declining towards the extinction horizon, or species that migrated away from the area prior to the extinction horizon due to shifting environmental conditions (MacLeod, 1996).

Statistical analysis of extinction patterns may help to compensate for the limitations of the fossil record. For example, the Stratigraphic Confidence Interval Technique developed by Strauss & Sadler (1989) and Marshall (1994) calculates error bars for the first and last appearances of species (MacLeod, 1996; Hallam & Wignall, 1997). However, this technique assumes that sampling was continuous (which often is not possible) and excludes rare species (Hallam & Wignall, 1997), and so may not be applicable to real data sets (see review by Smith, 1994, p. 119-121).

Another technique, which is being increasingly used in mass extinction studies, is graphical correlation (e.g. Armstrong, 1995; MacLeod, 1996). The Graphical Correlation Method was developed by Shaw (1964) and is outlined by Smith (1994, p. 117-119) and Armstrong (1995). The method involves the comparison of first and last appearances of common taxa between measured sections across a stratigraphic interval. This allows the maximum ranges of the taxa to be identified and the development of a standard reference section with which other sections can be compared. This method is useful for the identification of a general pattern of extinction within a single region. However, graphical correlation, if used globally and for sections in different environmental settings, may obscure spatial differences in the pattern of extinction. It is for this reason, and the lack of common taxa between sections, that the Graphical Correlation Method has not been used herein. As discussed by Hallam & Wignall (1997), the appearances and disappearances of taxa should not be regarded as occurring within a 'void'. The relationship between the appearances and disappearances of taxa and changes in the sedimentary and geochemical record can help to determine the mechanisms affecting the distribution of taxa.

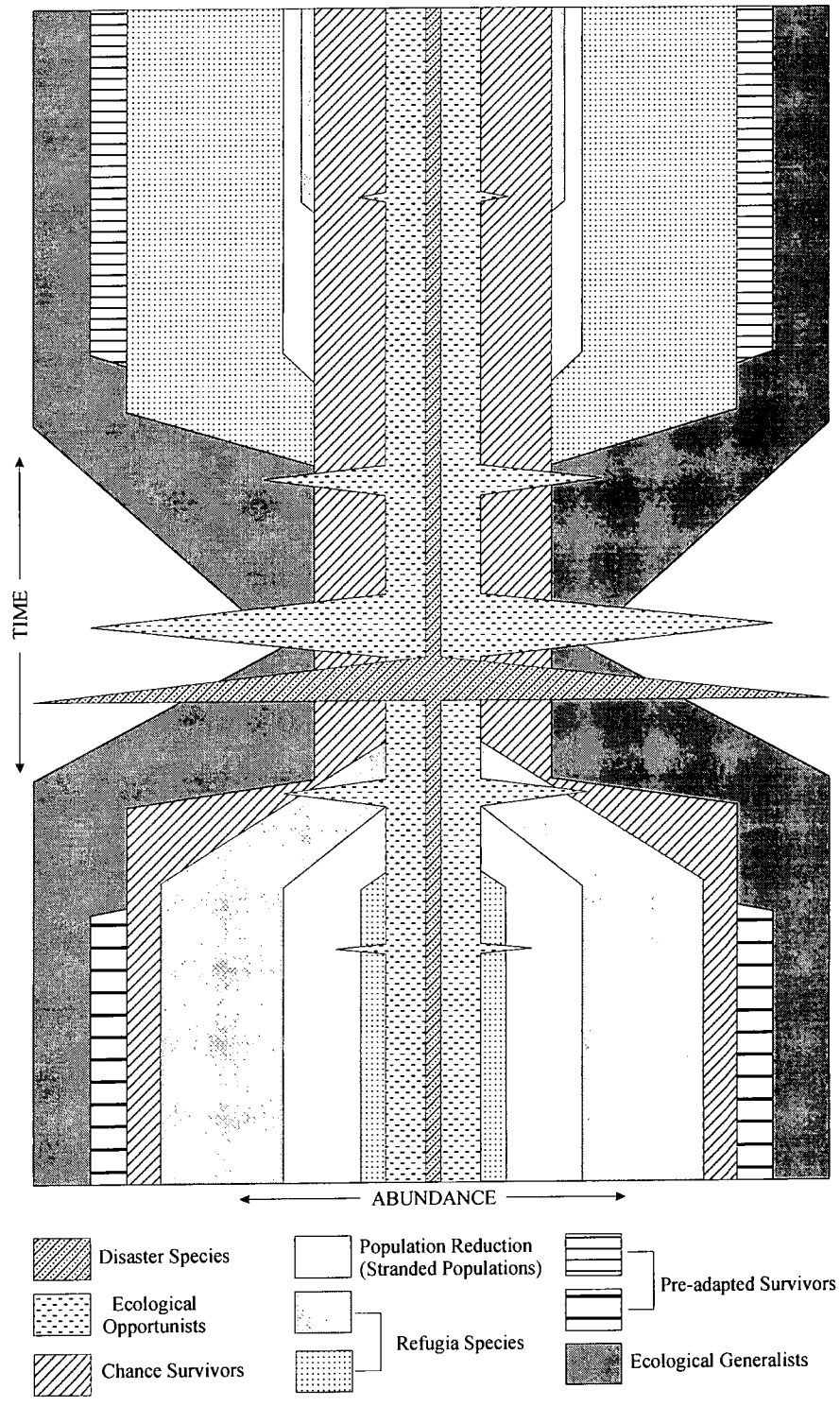


Figure 1.4 Composite Survival Model. The terms are defined in Section 1.8. Modified from Harries *et al.* (1996).

1.3 Survival

The preferential survival of ecological generalists or widespread taxa following mass extinction events has been suggested by many authors. Jablonski (1986) reported that survival mechanisms identified across background extinction events, were largely ineffective across the K/T mass extinction boundary, when the only survivors were from lineages that had been previously widespread, ecological generalists. However, Harries *et al.* (1996) argued that if survivors were limited to ecological generalists, recovery would be very slow and that rapid, explosive radiations could not be explained with so few survivors. They outlined survival mechanisms, which would allow a diverse rootstock from which rapid recovery could proceed (Figure 1.4). The effectiveness of the different survival mechanisms would be determined by the cause of the mass extinction event (Harries *et al.*, 1996).

1.4 Recovery

Following advances in the understanding of causal mechanisms and processes involved in mass extinction, research has started to focus on understanding the recovery of organisms following mass extinction events. This progress has been furthered by the initiation of an international working group (IGCP 335). Research has focused on completing high-resolution, interdisciplinary studies of key localities spanning mass extinction boundaries and the development of a standard terminology and recovery model (Kauffman & Harries, 1996; Figure 1.5).

Reviews of the current advances in recovery studies include those of Harries (1995) and Kauffman & Erwin (1995). The period of recovery may be discussed in terms of the initial appearance or reappearance of taxa following the extinction event (Initial Recovery Interval) and the long-term recovery of the biota (Long-term Recovery Interval).

1.4.1 Initial Recovery

The recovery model of Kauffman & Harries (1996; Figure 1.5) details the initial recovery of the biota. The pattern of appearance or reappearance of taxa immediately

following an extinction event may be explosive, gradual or stepwise (Harries, 1995). Harries (1995) suggested that gradual or stepwise recovery would result from the gradual amelioration of climatic conditions following the extinction event. However, it can also be suggested that the severity of the extinction event would affect the rate and pattern of recovery. As with extinction studies, the true recovery pattern may be difficult to identify. This is due to variations in sedimentation, the failure to recognise Lazarus Taxa and the forward smearing of the first appearance of new taxa (the reverse of the Signor Lipps Effect; Harries, 1995).

New taxa that appear following or during an extinction event often have a cryptic ancestry, but must have evolved prior to the extinction event or have descended from survivors of the extinction event (Harries, 1995). They may have evolved in situ or migrated from another area. For example, species may evolve in deep water and migrate on to the shelf during changes in environmental conditions: phylogenetic emergence (e.g. Cambrian trilobites; Stitt, 1977). The reverse process may also occur; this has been termed phylogenetic submergence (e.g. Devonian Trilobites; Feist, 1991).

The origination of species (speciation) following an extinction event results from the opening of ecospace, which may be filled by invading species. During periods of background extinction species within a niche (incumbents) can be replaced by other species (invaders) which are better adapted to that niche (displacive competition; Hallam & Wignall, 1997). However, the incumbent species would be well adapted to its niche and so would be more likely to be replaced when an environmental change, such as an extinction event, caused its demise (pre-emptive competition; Hallam & Wignall, 1997). The niche may then be filled by an invading species, which has preferential adaptations to those of contemporary species (incumbent replacement; Skelton, 1993; Hallam & Wignall, 1997).

Speciation during or following an extinction event may result from genetic divergence brought about when a population becomes geographically isolated (allopatric speciation; Charlesworth, 1990). An alternative method of speciation is sympatric speciation, which results from genetic isolation due to preferential mating within a spatially heterogeneous population, but this process is thought to be rare or non-

existent (Charlesworth, 1990). A less extreme method is that of parapatric speciation, in which speciation proceeds in populations that are only partially isolated. For example, two populations which are connected by a chain of adjacent populations may become reproductively isolated (Charlesworth, 1990). Differentiation between these three speciation mechanisms is difficult to ascertain from the fossil record.

1.4.2 Long-term Recovery

A model specifically detailing the processes of long-term recovery following an extinction event has not been developed. However, a number of evolutionary models have been developed to explain long-term trends in evolution. The Red Queen Model (Van Valen, 1973) predicts that evolution is driven by interactions between species and so is a constant process (Benton, 1990). Conversely, the Stationary Model (Stenseth & Maynard, 1984) predicts that evolution is sporadic, only occurring during periods of abiotic change (Benton, 1990). Alternative evolutionary theories include the Punctuated Equilibrium Theory of Gould & Eldredge (1993), which predicts that evolution proceeds as a series of rapid speciation events separated by periods of stasis. Conversely, the *Plus ça change* Model of Sheldon (1996) predicts that punctuated equilibrium will occur in widely fluctuating physical environments, and in less changing environments continuous gradualistic evolution would dominate.

Sheehan (1991) suggested that long periods of reorganisation followed mass extinction events, when lineages evolved new adaptations and moved into new ecological niches. He termed these periods Reorganisational Ecological Evolutionary Units (R.E.E.U.S). The R.E.E.U.s were separated by Stasis E.E.U.s, which represented relatively long periods of stability when evolution and speciation were constrained and lineages evolved within a specific ecologic niche (Sheehan, 1991, 1996). Sheehan (1991) suggested that mass extinction events caused changes in the history of lineages, destroyed established ecological associations and resulted in restructuring of communities. This thesis will concentrate on the recovery period following the end-Ordovician mass extinction event, which has been termed reorganisational E.E.U. V (Sheehan, 1991; Figure1.2).

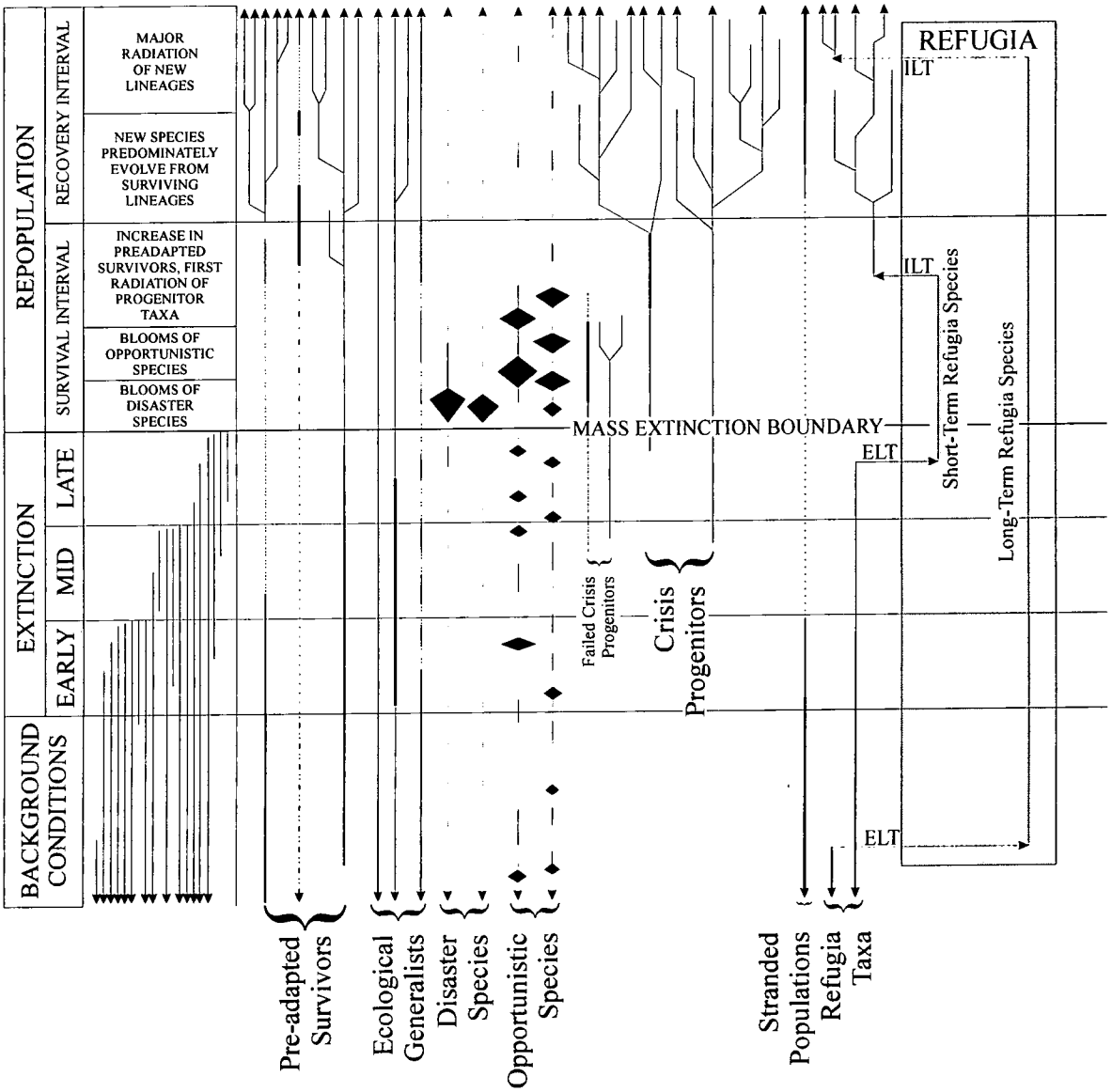


Figure 1.5 Model of survival and recovery from Kauffman & Harries (1996). For term definitions, refer to Section 1.8. ELT, Emigrant Lazarus Taxa; ILT, Immigrant Lazarus Taxa. The width of the solid lines depict the relative abundance of taxa and dotted lines represent intervals of non-occurrence. Arrows represent emigration or immigration of refugia taxa.

1.5 Extinction, Recovery and Macroevolution

The study of recovery is critical to our understanding of the evolutionary impact of mass extinction events (Harries, 1995). Macroevolution describes 'large scale genotypic / phenotypic change', whereas microevolution is concerned with the small-scale changes, on a generation by generation basis, resulting from 'natural selection and genetic drift' (Eldridge, 1990). The effect of mass extinction and recovery on macroevolution can be determined by studying diversity and the change of dominant faunas through time.

Sepkoski (1981) identified three Evolutionary Faunas through the Phanerozoic marine realm: Cambrian, Palaeozoic and Modern Faunas. The change in dominance of the Palaeozoic Fauna over the Cambrian Fauna is not associated with one of the five major mass extinction events. However, the demise of the Palaeozoic Fauna can be partially linked to the end-Permian mass extinction event. The elements of the Modern Fauna were little affected by the end-Permian extinction event whereas the Palaeozoic Fauna suffered a major decline in diversity. It has been suggested that increased predation and burrowing by elements of the Modern Fauna caused the failure of elements of the Palaeozoic Fauna to recover following the end-Permian mass extinction event. This hypothesis highlights the role that mass extinction and recovery have played in shaping life on Earth.

1.6 Conodonts

1.6.1 An Introduction

Conodont elements are phosphatic microfossils, typically 1mm in size. The history of conodont studies has been reviewed by Aldridge (1987) and Sweet (1988) and recent controversies have been discussed by Aldridge & Purnell (1996). Conodonts were first recorded in the literature in 1856 by the Russian palaeontologist, C. H. Pander (Sweet, 1988). Conodont elements were subsequently described and classified in terms of their general morphology (form taxonomy). The study of rare bedding-plane assemblages and statistical analysis of discrete elements led to the discovery that

elements of different shape actually occurred within the same species (e.g. Bergström & Sweet, 1966; Kohut, 1969). Consequently, multielement taxonomy was developed (e.g. Clark *et al.*, 1981). A suprageneric classification is now in place (e.g. Aldridge & Smith, 1993) and reconstructions of apparatus architecture have been developed for the Prioniodontida (Aldridge *et al.*, 1995; Figure A.2), Ozarkodinida (Purnell & Donoghue, 1998; Figure A.1) and the Panderodontida (Sansom *et al.*, 1995; Figure A.7).

Conodont elements can be described in terms of their morphology (general shape) and location within the apparatus. Two general shape categories have been identified (coniform and non-coniform; Sweet, 1988). Coniform elements are often termed 'simple cones', due to their conical shape (Sweet, 1988). Non-coniform elements (pectiniform and ramiform) have anterior, posterior and / or lateral processes extending from the main cusp (Sweet, 1988). The non-coniform architectural scheme comprises elements within three main locations (S, M and P elements; Sweet, 1988; e.g. Figure A.1, A.2). Although a consensus has not yet been reached regarding the locational nomenclature applied to coniform conodonts, a locational scheme has been developed for the Panderodontida, which may be applicable to other coniforms (Sansom *et al.*, 1995; Figure A.7).

From the moment that they were discovered, suggestions regarding the zoological affinities of the Conodonta have abounded, with suggestions ranging from algae to vertebrates (see Aldridge, 1987). The question of their affinity remained 'one of the most fundamental unanswered questions in systematic palaeontology' (Müller, 1981, referenced by Aldridge, 1987), until 1983 when conodont elements were found in association with soft-tissue preservation on bedding planes within the Carboniferous, Granton Shrimp Bed (Briggs *et al.*, 1983). Additional conodont animals have been recovered from Silurian (Mikulic *et al.*, 1985) and Ordovician strata (Aldridge & Theron, 1993; Gabbott *et al.*, 1995).

The conodont animal specimens have indicated a chordate affinity (Aldridge *et al.*, 1986) and histological study of conodont elements has suggested that they bore the earliest vertebrate hard tissues, which provides unequivocal evidence of their vertebrate affinity (Sansom *et al.*, 1992). Soft-part preservation in the conodont

animal specimens indicates that the animal had a notochord and chevron shaped muscle blocks and caudal fins (Aldridge *et al.*, 1993a). In the head region, two circular structures have been found, which are thought to represent sclerotic cartilages that were a support for the animal's eyes (Aldridge & Theron, 1993).

It is generally accepted that conodont elements functioned as the feeding apparatus of an extinct chordate (Aldridge & Purnell, 1996). However, it is not known whether the conodont animal was a microphagous suspension feeder (Nicoll, 1995) or a macrophagous predator (Briggs *et al.*, 1983; Purnell, 1995). Current studies indicate a grasping function for the S and M elements and a crushing and slicing function for the P elements, implying a macrophagous mode of life (see discussion in Aldridge & Purnell, 1996).

Attempts to explain the spatial distribution of conodonts have resulted in the development of two competing hypotheses: the Depth Stratification (Seddon & Sweet, 1971) and Lateral Segregation Models (Barnes & Fåhræus, 1975). Seddon & Sweet (1971) considered conodonts to be pelagic, but observed that conodont species were not uniformly distributed, as would be predicted if they were truly pelagic. They developed the Depth Stratification Model, which suggested that conodonts were pelagic, but inhabited different water depths. A flaw in this model is the fact that conodonts found in very shallow-water sediments are not usually found in all water depths, as would be expected (Sweet, 1988). However, Sweet (1988) suggested that conodont distributions in the fossil record could still be explained by the model if conodonts had not been ubiquitous within their preferred water layer, or if a number of species had inhabited the same water layer, but at different distances from the shoreline.

The alternative Lateral Segregation Model suggested that non-coniform genera had a benthic or nektobenthic habit, whereas coniform genera, which were independent of facies, had a pelagic mode of life (Barnes & Fåhræus, 1975). Sweet (1988) reviewed the two models and concluded that a general consensus regarding the validity of the models had not yet been reached. He suggested that conodont distribution was consistent with qualities of both models, and that the mode of life of conodonts varied from pelagic to nektobenthic.

Distinctive associations of conodont species can be linked to particular geographic areas (provinces) or particular environmental conditions (biofacies; e.g. Sweet & Bergström, 1984). Species within a biofacies were not necessarily limited to, but reached an acme within, that specific environment, and thus, determination of the percentage of a species within a fauna is vital if biofacies are to be quantified. Sweet & Bergström (1984) identified and defined a number of biofacies within the Upper Ordovician by calculating the percentage of each species within faunas from different geographic areas. The percentage of a species within a fauna was calculated by counting the number of elements of that species within a sample, and working out the percentage that that species represented of the total number of elements recovered. The percentages only represent an estimate of faunal composition, as the number of elements within an individual may have differed between conodont species.

A possible alternative method would be to calculate the number of a specific element (e.g. M element) of a species within a fauna, so that the number of individuals of each species could be estimated. However, analogous elements have not yet been identified in all apparatuses. The number of elements within each of the known conodont bauplans is as follows: Ozarkodinida (15 elements), Panderodontida (17 elements), Prioniodontida (19 elements). The number of elements are similar, and so the 'Sweet & Bergström' method may in fact be a good estimate for the composition of the fauna. This method has been used herein to calculate percentages of species within the samples collected, and from samples discussed in the literature.

The possible controls on the distribution of biofacies include temperature, light penetration and intensity, turbidity, energy, salinity and water density (Sweet & Bergström, 1984; Sweet, 1988). Sweet (1988) suggested that temperature was the critical control, as Ordovician conodonts common in high latitude, shallow waters were also common in deep water in lower latitudes, where the temperature would have been similar to that at high latitudes. Horizons within the ocean such as the seasonal and permanent thermoclines may have acted as barriers between conodont biofacies (Armstrong, 1996).

1.6.2 Upper Ordovician and Lower Silurian conodonts

In the Upper Ordovician, two broad, temperature related, conodont faunal regions have been documented: the Atlantic and Midcontinent Faunal Regions (Sweet & Bergström, 1984; Figure 4.4). The Midcontinent Faunal Region was typically developed on the North American and Siberian cratons, which were characterised by low-latitude, warm-water faunas (Sweet & Bergström, 1984). Typical genera included *Aphelognathus*, *Belodina*, *Gamachignathus*, *Oulodus*, *Phragmodus*, *Pseudobelodina*, and *Rhipidognathus* (Sweet & Bergström, 1984). The Atlantic Faunal Region comprised faunas that are common in high latitudes and cooler waters (Sweet & Bergström, 1984). Characteristic genera included *Hamarodus*, *Icriodella*, *Periodon* and a distinctive suite of coniform taxa (Sweet & Bergström, 1984). It should be noted here that ramiform and pectiniform taxa will be united under the term non-coniform taxa within the following chapters, whilst coniform taxa will be used to describe both coniform and rastrate taxa.

Species that occurred in both faunal regions included coniform genera such as *Drepanoistodus*, *Panderodus*, *Paraoistodus*, and *Protopanderodus* (Nowlan *et al.*, 1997). The non-coniform genus *Amorphognathus*, although indicative of the Atlantic Faunal Region earlier in the Ordovician, became common in the Midcontinent Faunal Region in the uppermost Ordovician (Nowlan *et al.*, 1997).

Variations in conodont faunas within the faunal regions occurred and have been attributed to biofacies associated with depth (Sweet & Bergström, 1984). Within the *velicuspis* Chron, Sweet & Bergström (1984) identified a number of depth-related biofacies in sections marginal to Laurentia (Figure 4.4). The *Aphelognathus-Oulodus*, *Pseudobelodina*, *Plectodina* and *Phragmodus undatus* Biofacies were identified on the shelf and comprise faunas indicative of the Midcontinent Faunal Region (Figure 4.4). An *Amorphognathus superbus - ordovicicus* Biofacies was identified at the shelf edge, and a *Dapsilodus mutatus - Periodon grandis* Biofacies in deeper water close to the Carbonate Compensation Depth (CCD), which comprised taxa typical of the Atlantic Faunal Region.

In the Lower Silurian similarities between North American and European faunas led Sweet (1985) to suggest that differences between cool- and warm-water faunas had disappeared, with only minor variations in conodont faunas existing across the shelf (Aldridge, 1976; Le Fèvre *et al.*, 1976; Aldridge & Mabillard, 1981). Faunas recovered from Lower Llandovery shelf sections were dominated by *Panderodus,* in association with *Distomodus*, *Icriodella*, *Kockelella*, *Oulodus*, and *Ozarkodina* (Armstrong, 1990; Watkins & Kuglitsch, 1997).

The study of the conodont fauna from outer shelf - slope sections in Greenland led to the identification of a low-diversity slope fauna. Armstrong (1990) described the 'slope and outer-shelf biofacies' as being dominated by *Dapsilodus*, *Decoriconus*, and *Pseudolonchodina.* A slope fauna was subsequently identified in the outer shelf - slope sections in the Canadian Cordillera ('*Aspelundia* – *Dapsilodus* fauna'; McCracken, 1991b) and the Michigan Basin ('Offshore Biofacies'; Watkins & Kuglitsch, 1997), but they differed slightly in composition from the biofacies described by Armstrong (1990). The 'Offshore Biofacies' described by Watkins & Kuglitsch (1997) was dominated by *Panderodus*, *Pseudolonchodina*, and *Walliserodus,* whilst that of McCracken (1991b) was also dominated by *Dapsilodus* (15%). All three of the slope faunas discussed have one dominant genus in common though, which is *Pseudolonchodina.*

In summary, a Shelf Biofacies and a Slope Biofacies can be identified in Lower Silurian conodont faunas. The apparent uniformity of Llandovery faunas suggested by Sweet (1985) was a consequence of the virtual lack of conodont studies based on higher-latitude or deeper-water environments and on palaeocontinents other than Laurentia, Avalonia and Baltica (Sweet, 1985; Bergström, 1990).

Variation of the species found within a biofacies can occur between provinces. A number of provinces were identified within the Upper Ordovician 'Atlantic Faunal Region' (British, Baltic and Mediterranean Provinces; Bergström, 1990) and the 'Midcontinent Faunal Region' (Red River, Ohio Valley, Siberian and Austral-Asian Provinces; Sweet & Bergström, 1984; Nowlan *et al.*, 1997). Provinces have not been formally recognised in the Lower Silurian. However, variation in the faunas recovered

from Laurentia, China and Australia indicate that conodont taxa in a similar environmental setting did vary slightly in different geographic areas.

It can be noted from the discussion above that the same biofacies has been described by different names at different periods of time and during the same period of time by different workers. This has resulted from the difficulty in finding suitable names for biofacies. Biofacies may be named after dominant species/genera, an assemblage of species/genera, or the particular environment within which the distinctive fauna is found. However, there are problems associated with each of these methods. If a biofacies is named after a dominant species or genus, the name may become no longer applicable if the species or genus dies out, whilst the biofacies continues to occupy the same environmental niche. The name may also not be applicable to a similar biofacies in a different geographic setting, due to provincialism.

Problems may arise if a biofacies is named after an environment, such as shelf or slope, as a biofacies found in deep water at low latitudes may occur in shallower water at high latitudes. In this circumstance, the biofacies could be named after the principal controlling factor, which is thought to be temperature. However, estimating the temperature of the water that a particular biofacies occurred within would be difficult. The method of naming the biofacies after the environment within which it is found is favored herein, as the dominant taxa in the Ordovician are different from those that dominated in the Silurian, and so the name of a species is not relevant to both periods of time. The names given to biofacies in low latitudes may not be appropriate for those found in higher latitudes. The study herein is mainly based on conodont data from low latitudes. The biofacies terminology used in this study is outlined below.

The Shelf Biofacies in the Upper Ordovician is dominated by, *Aphelognathus*, *Oulodus*, *Pseudobelodina*, *Plectodina* and *Phragmodus*. Whereas, in the Lower Silurian the shelves were dominated by *Panderodus,* in association with *Distomodus*, *Icriodella*, *Kockelella*, *Oulodus*, and *Ozarkodina*. In the Upper Ordovician, the Slope Biofacies was dominated by *Dapsilodus* and *Periodon,* and in the Lower Silurian the dominant taxa included *Pseudolonchodina*, *Dapsilodus*, *Walliserodus*, *Decoriconus* and *Panderodus*. In the Upper Ordovician a biofacies dominated by *Amorphognathus*

was found at the shelf edge and this will be referred to as the Shelf-edge Biofacies (Sweet & Bergström, 1984). Additional biofacies whose existence is implied by the fossil record, but have not actually been identified within a particular area or environment, may be named after the dominant taxa. The biofacies identified across the Upper Ordovician shelf by Sweet & Bergström (1984) will be regarded as sub-biofacies of the Shelf Biofacies. In basic terms, the Shelf Biofacies equates to the Midcontinent Faunal Region and the Slope Biofacies to the Atlantic Faunal Region of Sweet & Bergström (1984).

1.7 The end-Ordovician mass extinction event

The end-Ordovician mass extinction event caused the disappearance of 12% of all Ordovician families (Raup & Sepkoski, 1982; Figure 1.1) and affected a wide range of faunas (see review by Brenchley, 1990). It was one of the most striking conodont extinction events in their 400 million year history (Sweet, 1985; Barnes & Bergström, 1988; Aldridge 1988; Figure 1.3). Conodont extinctions occurred gradually through the Ashgill with a short, intense, interval of extinction in the latest Ashgill (Barnes & Bergström, 1988).

Glacial deposits and major regression within the Upper Ordovician indicate a link between the extinction event and the initiation of glacial conditions in a previously greenhouse world (Hambrey, 1985). The identification of a positive $\delta^{18}O$ and $\delta^{13}C$ isotope excursion within the Hirnantian (uppermost stage of the Ordovician) suggested that the glacial conditions prevailed. The interpretation of the positive $\delta^{18}O$ and $\delta^{13}C$ isotope excursions are discussed in detail in Section 1.7.1. The excursions suggest that glacial conditions were confined to a period of approximately 1 million years (Marshall & Middleton, 1990; Brenchley *et al.*, 1994; Section 1.7.1). In contrast, evidence from glacial deposits, sea level and changes in lithology, suggest that the glaciation was actually initiated during the early Ashgill and not within the uppermost Ashgill (Hirnantian; Armstrong & Coe, 1997). Herein the period of time represented by the $\delta^{18}O$ and $\delta^{13}C$ positive excursions will be referred to as the end-Ordovician glacial maximum, as cooling may have been initiated prior to this.

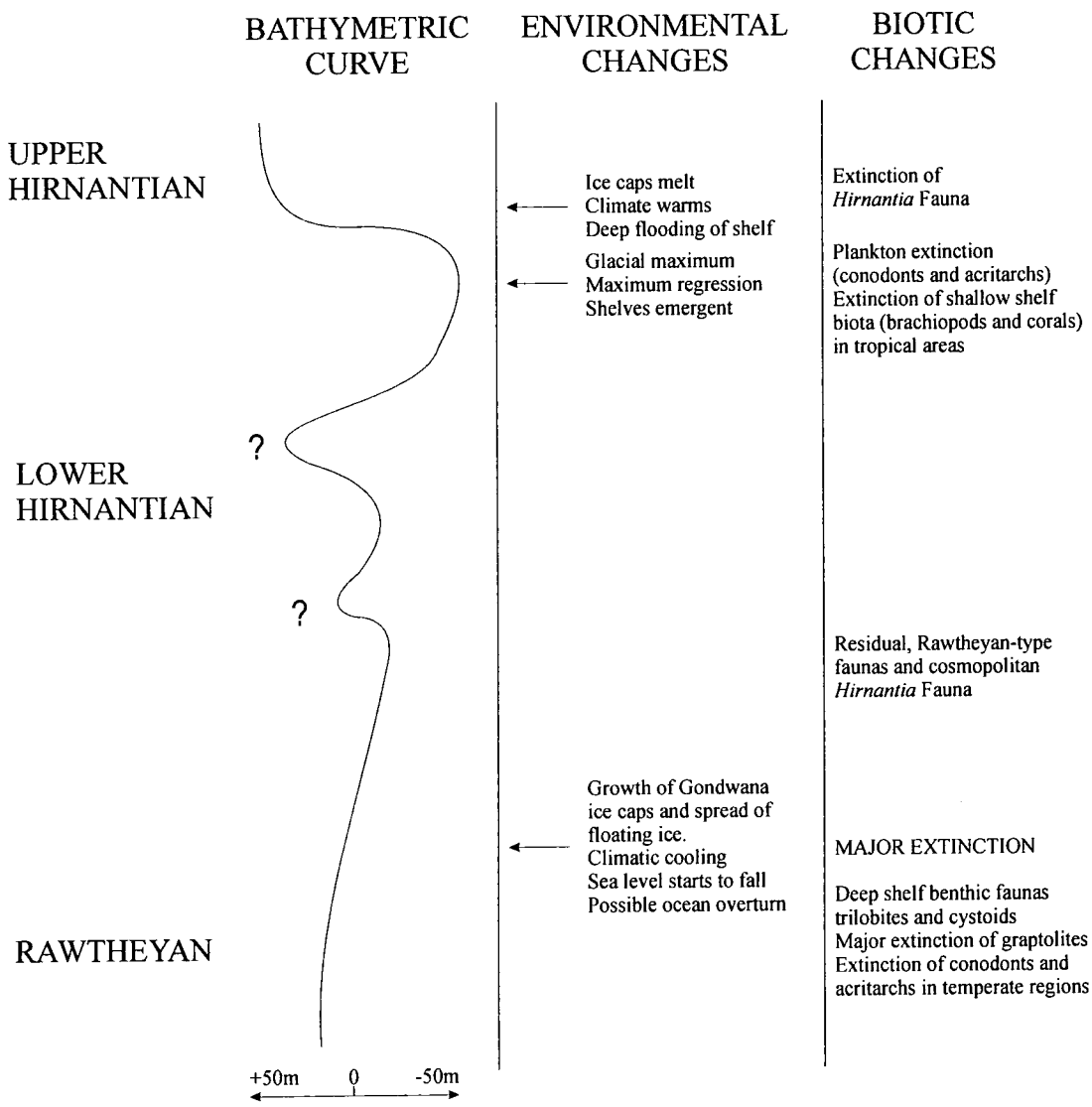


Figure 1.6 Biotic and environmental changes of the end-Ordovician glacial maximum.

It has been suggested that two strikes of extinction would have occurred, linked to the onset and subsequent cessation of the glacial maximum (Brenchley *et al.*, 1995; Figure 1.6). However, few studies have concentrated on correlating the climatic changes with the actual fossil record. Thus, the exact timing of the latest Ashgill extinction events has not been determined and although linked to the glaciation, the actual causal mechanisms have not yet been proven.

1.7.1 The $\delta^{18}O$ and $\delta^{13}C$ isotope excursion

Ancient $\delta^{18}O$ values can be obtained from diagenetically unaltered brachiopod valves and whole rock analysis of limestones. Fractionation between ^{18}O and ^{16}O is temperature dependent, with an inverse relationship existing between $\delta^{18}O$ and temperature (Epstein *et al.*, 1951; Marshall, 1992). ^{16}O is lighter than ^{18}O and is preferentially taken out of the oceans during evaporation. The ^{16}O rich water returns to the ocean via precipitation unless trapped in continental ice. Therefore, during times of glaciation, $\delta^{18}O$ rises.

Alternative interpretations have also been made. For example, Railsback (1990) suggested that a $\delta^{18}O$ positive excursion may also have resulted from salinity stratification of the oceans. $\delta^{18}O$ would vary with evaporation rate. A high rate of evaporation would create highly saline waters in low latitudes, which were enriched in ^{18}O. The dense saline water would sink and remain isolated beneath the pycnocline resulting in a more positive $\delta^{18}O$ ratio in the shallow seas. Therefore, excursions in $\delta^{18}O$ can indicate periods of change in temperature, ice volume, and / or oceanic circulation.

$\delta^{13}C_{inorganic}$ can be obtained from whole rock samples of limestone or brachiopod valves and $\delta^{13}C_{organic}$ can be obtained from whole rock samples of organic, kerogen-rich shales (Marshall, 1992; Popp *et al.*, 1997). $\delta^{13}C$ increases with increasing oceanic productivity as ^{12}C is preferentially taken up by organisms. Various workers (Jenkyns *et al.*, 1994) have related $\delta^{13}C$ to changes in sea level. Transgressive events increase the area of the shallow-shelf seas where the majority of organic carbonate is

synthesised. This results in a positive shift in $\delta^{13}C$. It has also been suggested that variations in $\delta^{13}C$ reflect changes in ocean surface water CO_2 (see references in Wang *et al.*, 1997). For example, an increase in $\delta^{13}C$ may reflect decreased CO_2 in surface waters (Marshall, 1992). Increased burial of organic matter (e.g. in black shales) would cause a positive $\delta^{13}C$ excursion and indicate anoxic bottom waters (Marshall, 1992). In summary, changes in $\delta^{13}C$ may indicate changes in sea level, biomass and burial of organic matter.

It can be argued that during a glaciation, regression would be accompanied by a positive $\delta^{18}O$ excursion, due to decreased temperature and increased ice volume (Marshall, 1992). Additionally, a negative $\delta^{13}C$ excursion would occur due to the decrease in the area of the shallow shelf, and thus a reduction in the synthesis of organic carbonate. However, at the end of the Ordovician, the $\delta^{18}O$ positive excursion is associated with a positive $\delta^{13}C$ excursion, rather than a negative $\delta^{13}C$ excursion as would be predicted (Brenchley *et al.*, 1994). The positive shift in $\delta^{13}C$ during a time of cooling has been interpreted as representing changes in carbon cycling in the oceans (Brenchley *et al.*, 1995). Brenchley *et al.* (1995) interpreted the positive carbon isotope shift as an increase in plankton productivity or organic carbon storage in sediments. In summary, the coincident positive $\delta^{18}O$ and $\delta^{13}C$ excursions are currently interpreted as representing glacial conditions in the uppermost Ordovician.

1.8 Glossary — Recovery Terminology

The definitions below are those outlined by Kauffman & Harries (1996; Figure 1.4)

Crisis-Progenitor Taxa

Taxa that are adapted to the environmental conditions of the mass extinction interval, and so readily survive the extinction event. They are among the first groups to seed radiation into unoccupied ecospace.

Disaster Species

Taxa that are specially adapted to extreme environments. Disaster Species are normally absent or rare in stable environments, but may occur as short-lived population blooms after an extinction event.

Ecological Generalists (Eurytopic Taxa)

Taxa that can tolerate changes in environmental factors and can inhabit many ecological niches. They have long stratigraphic ranges, slow evolutionary rates and often have primitive morphological features. They may represent ancestral stocks within clades. They are not abundant in stable communities but become dominant during extreme conditions and so are common survivors of extinction events.

Ecological Opportunists

Taxa that inhabit minor ecological roles. They occur sporadically during environmental stability, but have short-lived population blooms during periods of environmental change.

Lazarus Taxa

Taxa that appear to become extinct at a mass extinction boundary, but reappear higher in the section.

Long-Term Refugia Species

Taxa which are forced into refugia by environmental change or competition in their primary habitat prior to the start of stressed environments associated with mass extinction. When this environmental change or competition is removed (after the extinction event), the Long-Term Refugia Species may return to the primary habitat as the same species or as new, phylogenetically related species due to evolution occurring in the refugia habitat.

Preadapted Survivors

Preadapted Survivors can normally adapt to minor changes in environmental conditions using survival mechanisms, which they may also use during the stressed conditions of mass extinction events. Preadapted Survivors are less abundant during mass extinction but expand again in the late survival and recovery intervals.

Refugia

Refugia protect species from environmental changes that lead to mass extinction of taxa in more exposed primary habitats.

Short-Term Refugia Species

Taxa which are forced into refugia habitats by the stressful environmental conditions during mass extinction events. As environmental conditions ameliorate, they rapidly return to their original habitats, without speciation occurring.

Stranded Populations

Widely dispersed species. Populations are greatly reduced during mass extinction and early recovery, but then expand again during the post-extinction return to normal environments. Stranded Populations may be confused with Lazarus Taxa. However Stranded Populations always remain within their primary habitat, whereas Lazarus Taxa are found in facies representing the non-primary habitats in which they can survive a mass extinction (i.e. refugia).

Other terms used in the study of recovery, which have not been used by Kauffman & Harries (1996) include:

Elvis Taxa

A species that appears during recovery that closely resembles a species that became extinct during the mass extinction event.

Chapter 2

Correlation of Ordovician and Silurian strata

Chapter 2

Correlation of Ordovician and Silurian strata

2.1 Introduction

Correlation involves the establishment of time-equivalent stratigraphic units and has been traditionally based on biostratigraphical range data. The time resolution of a biozone, the basic unit of biostratigraphy, averages 1-2 Ma and a biozone may encompass an error of about 1Ma (Miall, 1992). This degree of resolution is inadequate to correlate an increasing number of geological events and apparently instantaneous geochemical and sequence stratigraphical indices are being utilised to correlate with a resolution of less than 1Ma. Geological 'events' identified by geochemical and sequence stratigraphical approaches are also now being utilised in the study of correlation.

Correlation of Lower Palaeozoic rocks has been debated since the time of Murchison and Sedgwick in the early nineteenth century (see Holland, 1989). Many problems still exist, compounded by variations in the biostratigraphical data available between palaeogeographically separate sections. Traditionally, graptolites have been used to subdivide series and stages within the Ordovician and Silurian. Although common in deeper-water sediments, graptolites are rare within shallow-water carbonates, where conodonts are abundant and useful for correlation. Gaps in the sedimentological record have also been a major stumbling block, particularly in the correlation of the Ordovician-Silurian boundary. Upper Ordovician and Lower Silurian sea-level curves have been produced by many authors in different areas, but the lack of a high-resolution biostratigraphical framework has hindered the elucidation of their global extent.

This chapter aims to review the current biostratigraphical data available for the Upper Ordovician and Lower Silurian. A standard biostratigraphical framework has been

developed, to allow correlation of local and global sea-level cycles in the Upper Ordovician to Lower Silurian. Published chemostratigraphical data have also been added to the 'event' stratigraphical framework and are useful for correlation and / or the identification of episodes of climate change.

2.2 Chronostratigraphy

The uppermost series of the Ordovician System in Britain, the Ashgill, is subdivided into the Pusgillian, Cautleyan, Rawtheyan and Hirnantian Stages (Figure 2.1), and has an estimated duration of 4Ma (Barnes, 1992). The basal stratotype of the Ashgill is an outcrop of the Cautley Mudstone Formation at Foggy Gill, Cumbria (Fortey *et al.*, 1995). The base is identified by a change in the shelly faunas, but cannot yet be defined on the first appearance of a conodont or graptolite species. The base occurs within the *linearis* Graptolite Biozone (GBZ) and the *superbus* or *ordovicicus* Conodont Biozones (CBZ; Barnes, 1992; Fortey *et al.*, 1995).

Within this thesis, emphasis will be placed on correlation of the top Rawtheyan and Hirnantian Stage, as it was during this time that the main phases of the end-Ordovician mass extinction occurred (Brenchley *et al.*, 1995). The Hirnantian Stage has an estimated duration of 0.5Ma (Barnes, 1992). Its traditional type section is an outcrop of the Foel y Dinas Mudstones (Bala, Wales), a section which is poorly fossiliferous and considered to be unsuitable as a basal stratotype (Williams *et al.*, 1972). The Hirnantian Stage has not yet been formally defined, but Hirnantian strata has been identified traditionally by the presence of a distinctive shelly fauna, the *Hirnantia* Fauna; the base of the Hirnantian Stage is commonly taken as the first appearance of that fauna. The relationship between the base of the Hirnantian and the standard graptolite biozonation is uncertain (Section 2.3.3), but is widely depicted as occurring within the uppermost *pacificus* GBZ (e.g. Fortey *et al.*, 1995; Štorch & Loydell, 1996). The top of the Hirnantian Stage was originally defined by the disappearance of the *Hirnantia* Fauna. However, the stage concept has been extended to include the *persculptus* GBZ following the formal definition of the base of the Silurian (Fortey *et al.*, 1995). The stage now spans at least the *extraordinarius* (lower Hirnantian) and *persculptus* GBZs (upper Hirnantian; see Marshall *et al.*, 1997).

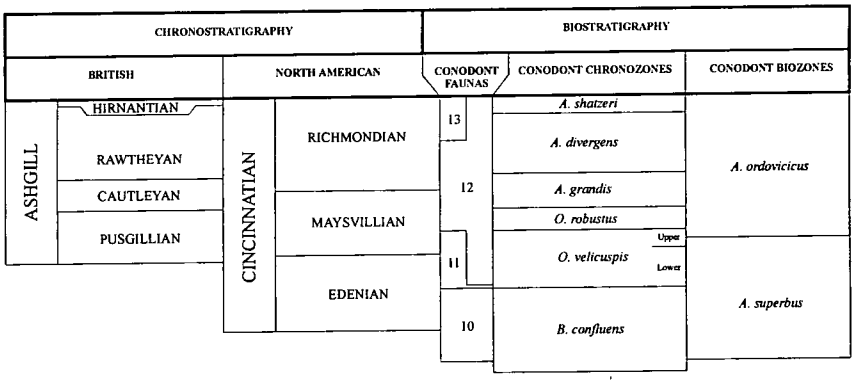


Figure 2.1 Upper Ordovician chronostratigraphy and conodont biozonation. After Sweet & Bergström (1984).

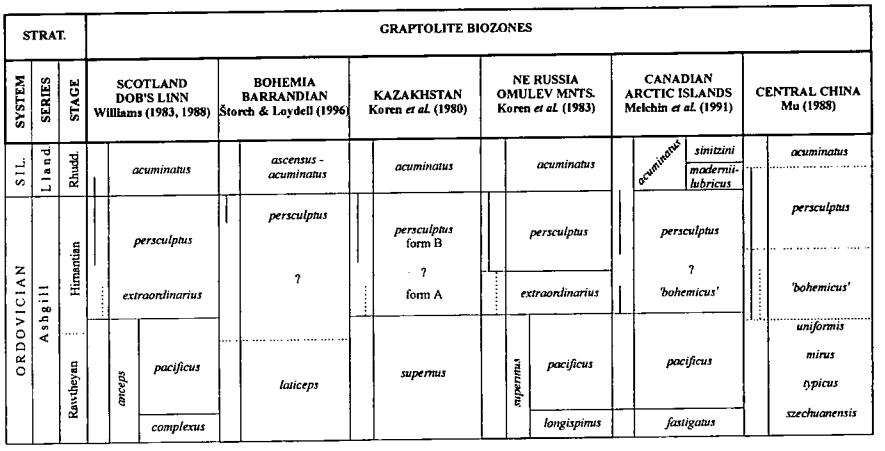


Figure 2.2 Correlation of uppermost Ordovician graptolite biozones. From Štorch & Loydell (1996). The range of *Normalograptus persculptus* is depicted by a solid line and the range of *Normalograptus extraordinarius* is depicted by a dotted line.

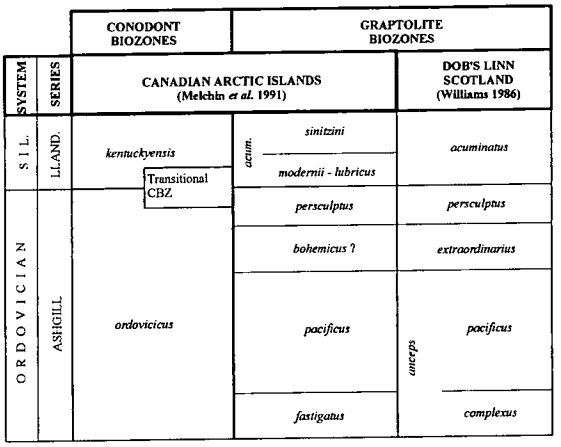


Figure 2.3 The biostratigraphical framework for the Upper Ordovician and Lower Silurian.

In North America, the uppermost series of the Ordovician System has been termed the Cincinnatian and can be divided into three stages: Edenian, Maysvillian and Richmondian (Figure 2.1). Correlation of the British and North American schemes indicates that the base of the Pusgillian Stage (base of the Ashgill) lies close to the base of the Maysvillian Stage (Barnes, 1992) and that the Hirnantian Stage correlates with the uppermost Richmondian Stage.

A fourth stage, the Gamachian, was proposed by Schuchert & Twenhofel (1910) following fieldwork on Anticosti Island (Québec). It encompasses strata thought to be younger than the Richmondian, but older than the Rhuddanian (basal Silurian; Lespérance, 1985; McCracken & Nowlan, 1986). The Gamachian was used only locally until formally re-established in 1981, when McCracken & Barnes (1981) recognised a distinctive conodont faunal assemblage (Fauna 13) on Anticosti Island, which had the potential to allow identification of the Gamachian in other regions (Section 2.3.2). However, Fauna 13, and hence the Gamachian Stage, have not been confidently identified in any sections other than those on Anticosti Island and so the Gamachian Stage cannot be used as a formal subdivision of the Cincinnatian Series (see Amsden & Barrick, 1986).

The Gamachian has also been used in the literature to describe the uppermost Ordovician strata on Laurentia bearing the *Hirnantia* Fauna (e.g. Ross & Ross, 1992, fig. 1; Holland & Patowsky, 1996), but in the light of the difficulties in correlation this seems premature. The lower Hirnantian Stage is preferred herein for strata that bear the *Hirnantia* Fauna, or can be correlated with strata bearing the *Hirnantia* Fauna.

The Hirnantian is followed by the Rhuddanian Stage of the Llandovery Series, Lower Silurian. The base of the Silurian has been formally defined (Holland, 1989). Two possible Ordovician-Silurian boundary stratotypes were proposed: the deep-water, graptolitic section at Dob's Linn (Scotland), or the shallow-water section bearing conodonts on Anticosti Island (Canada). At Dob's Linn, the boundary could have been placed at the base of the *persculptus* GBZ or the *acuminatus* GBZ. The base of the *persculptus* GBZ had traditionally been taken as the base of the Silurian, but the *acuminatus* GBZ was preferred as it allowed the boundary to be placed above the

Hirnantia Fauna, whose age range is uncertain (Holland, 1989). On Anticosti Island, the first appearance of the conodont *Ozarkodina oldhamensis* marked the proposed boundary horizon (Barnes, 1988; Holland, 1989). This boundary was not chosen due to the historical precedence of graptolites, and the perceived difficulty in applying a boundary defined on conodont species globally (Holland, 1989). Thus, the base of the Silurian System has been internationally defined by the base of the *acuminatus* GBZ at Dob's Linn (Cocks, 1985). This decision has met with some criticism, as in shelly sequences no evolutionary events were thought to coincide with the base of the *acuminatus* GBZ (Lespérance, 1985; Lespérance *et al.*, 1987a). However, it has been recently suggested that the base of the *kentuckyensis* CBZ is almost coincident with the base of the *acuminatus* GBZ, and may prove useful in identifying the base of the Silurian in shelly successions (Melchin *et al.*, 1991).

The basal series of the Silurian, the Llandovery Series has a stratotype defined in the Llandovery area, Dyfed, Wales (see Cocks, 1989). An alternative series name, the Anticostian, was proposed by McCracken & Barnes (1981) and Barnes (1989) with the associated stratotype on Anticosti Island. Stages within the Anticostian were defined by conodont appearances, but uncertainty surrounding the global applicability of conodont appearances led to the preference of the Llandovery Series (Holland, 1989). The duration of the Llandovery has been estimated at 13 Ma (Hughes, 1995). It is divided into three stages: Rhuddanian, Aeronian and Telychian. The base of the Aeronian has been formally placed at the base of the *triangulatus* GBZ and the base of the Telychian was placed at the base of the *turriculatus* GBZ (Holland, 1989). However, the *turriculatus* GBZ has now been revised and subdivided into the *guerichi* and *turriculatus-crispus* GBZs (e.g. Subcommission on Silurian Stratigraphy, 1995; Loydell, 1998; Figure 2.6). The base of the Telychian coincides with the base of the *guerichi* GBZ, and can also be identified by the appearance of the brachiopods *Eocoelia curtisi* and *Stricklandia laevis* at the type locality (Holland, 1989).

The stage boundaries have not been traditionally defined using conodont biozones. The base of the *kentuckyensis* CBZ is thought to occur near to the base of the *acuminatus* GBZ (Melchin *et al.*, 1991), which corresponds with the base of the Rhuddanian. The base of the Aeronian does not correspond with the base of a conodont biozone, and occurs within the *kentuckyensis* CBZ. The base of the *celloni*

CBZ has been shown to occur within the *turriculatus* GBZ (prior to its division into the *guerichi* and *turriculatus-crispus* GBZs). Therefore, indicating that the base of the *celloni* CBZ is near to the base of the Telychian. On Anticosti Island, the first appearance of *Eocoelia curtisi* occurs just prior to the base of the *celloni* CBZ (Jin *et al.*, 1996), and is coincident with the appearance of a distinctive conodont species, *Aulacognathus bullatus*, which may in future prove useful in correlation.

The Wenlock Series comprises the Sheinwoodian and Homerian Stages. The Wenlock has an estimated duration of 4Ma (Hughes, 1995). Its base lies close to the base of the *centrifugus* GBZ and within the *amorphognathoides* CBZ. The global standard for the base of the Wenlock Series is at Wenlock, Shropshire (see Bassett, 1989a).

2.3 Biostratigraphy

2.3.1 Graptolite Biozonation of the Upper Ordovician-Lower Silurian

Graptolites have been traditionally used to define stage and series boundaries within the Upper Ordovician and Lower Silurian. They are common in deeper-water shales, but rare within shallow-water carbonates. At Dob's Linn, the uppermost Ordovician to lowermost Silurian graptolite succession includes the *pacificus*, *extraordinarius*, *persculptus* and *acuminatus* GBZs (Williams, 1988). This biozonal scheme has been widely used, but a number of local biozonal schemes have also become established. A comparison of the various published schemes is presented in Figure 2.2.

One of the more widespread variations is the occurrence of the *bohemicus* GBZ, between the *pacificus* and *persculptus* GBZs, in the Chinese, Canadian and Bohemian sections. The *bohemicus* GBZ was regarded as equivalent to the *extraordinarius* GBZ, until *Glyptograptus bohemicus* and *Normalograptus persculptus* were synonymised by Štorch & Loydell (1996). The discontinuation of the usage of the *bohemicus* GBZ has now been recommended (Štorch & Loydell, 1996). These authors also suggested that in sections where *Normalograptus persculptus* first appears above the *extraordinarius* GBZ, the interval between the *extraordinarius* and *acuminatus* GBZs be termed the *persculptus* GBZ. In sections where the ranges of *Normalograptus*

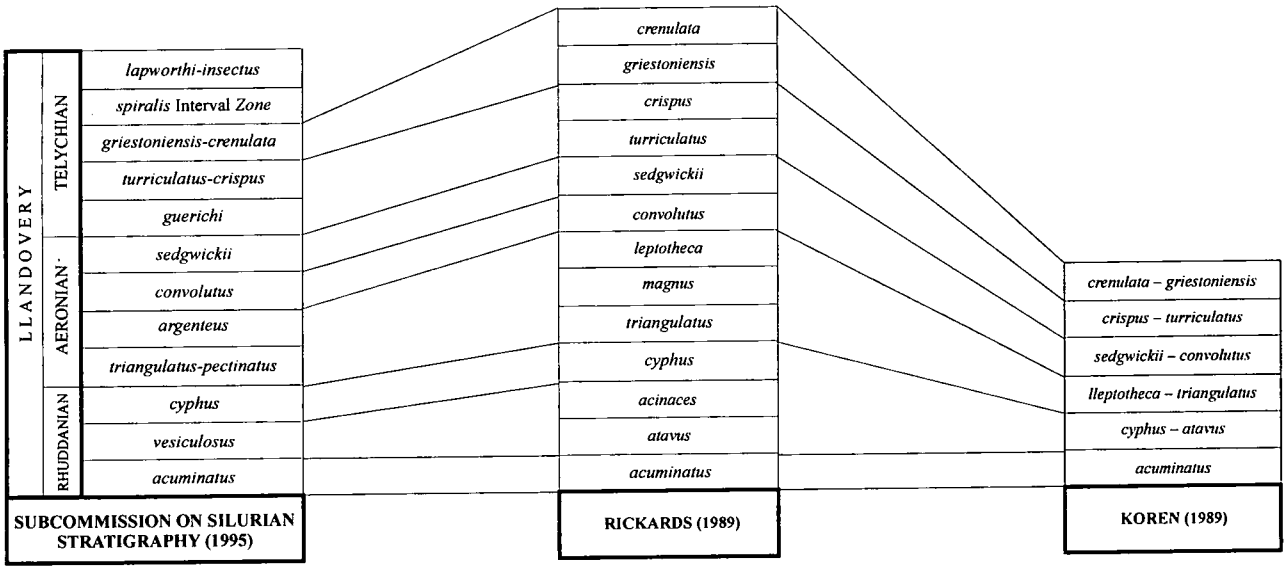


Figure 2.4 Correlation of the proposed standard graptolite biozonal schemes for the Llandovery.

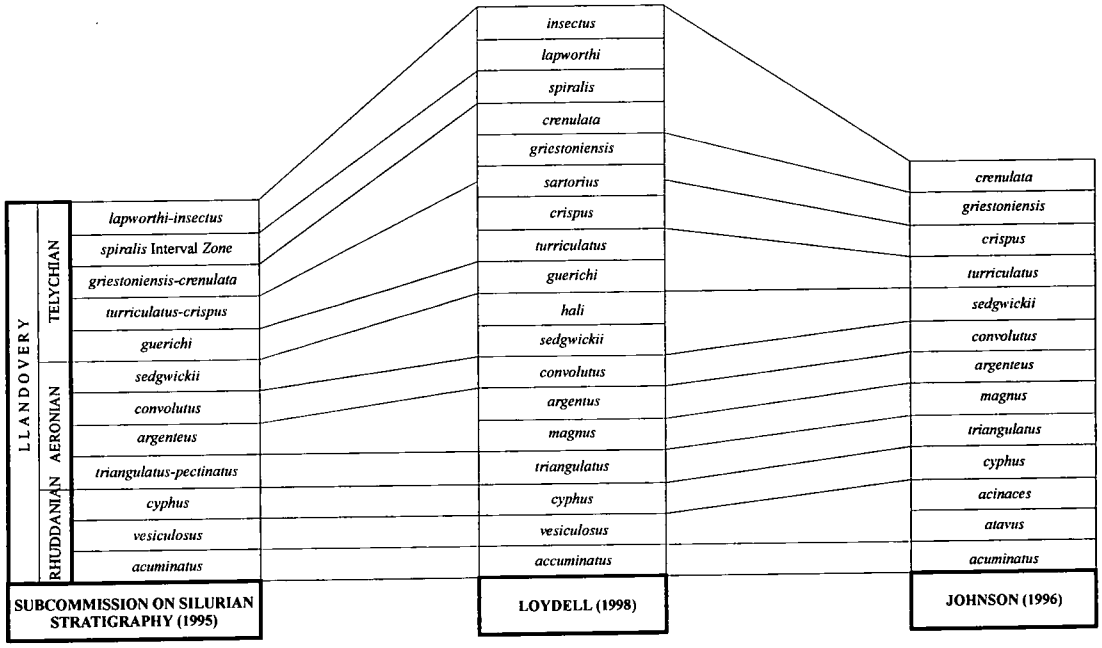


Figure 2.5 Correlation of the standard graptolite biozonal scheme and schemes used in sea-level studies.

persculptus and *Normalograptus extraordinarius* overlap, the lower part of the *persculptus* GBZ should be referred to as the *extraordinarius* Sub-biozone, of the *persculptus* GBZ. The base of the *persculptus* GBZ appears to be diachronous (Štorch & Loydell, 1996).

The creation of a standard graptolite biozonal scheme for the Llandovery has been equally problematical. The biozonal scheme of Rickards (1989) based upon the succession in Britain was not a formally agreed standard, but became widely applied, along with many local biozonal schemes (Loydell, 1993; Rickards, 1995). The schemes were variably composed of a mixture of range and assemblage biozones, some with ill-defined boundaries, and so caused difficulty in correlation (Koren *et al.*, 1995).

The most pronounced variation between biozonal schemes was observed within the Telychian (see Loydell, 1993). The Rickards (1989) scheme included only the *crenulata* GBZ in the upper Telychian, whereas in other regions up to four biozones were identified between the *crenulata* GBZ and the *centrifugus* GBZ (base of the Wenlock; Loydell, 1993; Figure 2.4). It has been suggested that the full succession of biozones was not identified by Rickards (1989), as upper Telychian strata in Britain lack graptolites (Loydell, 1993). To clarify the situation, the Subcommission on Silurian Stratigraphy (1995) proposed a biozonal scheme based upon the combined species range data from sections in Britain, Bohemia, Poland, South Tien Shan, China and Canada (Figure 2.6). This is currently used as the standard graptolite biozonal scheme for the Silurian and will be used throughout this thesis.

2.3.2 Conodont Biozonation of the Upper Ordovician – Lower Silurian

In the Ordovician, two distinct conodont faunal regions occurred (Midcontinent and Atlantic Faunal Regions) for which separate biozonal schemes have been developed (Bergström, 1990). The Atlantic Faunal Region includes taxa that are common in high latitudes and cooler water (Bergström, 1990). The Ashgillian biozonal scheme for the Atlantic Faunal Region is based on the first appearances of *Amorphognathus superbus* and *Amorphognathus ordovicicus* (Figure 2.1), but the exact position of the *superbus*

STRAT.			GRAPTOLITE BIOZONES	CONODONT BIOZONES
SILURIAN	WENLOCK	SHEINWOODIAN	*rigidus-perneri*	NOT ZONED
			riccartonensis-belophorus	*O. sagitta rhenana - K. patula*
			centrifugus-murchisoni	*K. ranuliformis* Interval *Zone*
	LLANDOVERY	TELYCHIAN	*lapworthi-insectus*	*P. amorphognathoides*
			spiralis Interval *Zone*	
			griestonensis-crenulata	*P. celloni*
			turriculatus-crispus	
			guerichi	*D. staurognathoides – P. tenuis*
		AERONIAN	*sedgwickii*	
			convolutus	
			argenteus	
			triangulatus-pectinatus	
		RHUDDANIAN	*cyphus*	*D. kentuckyensis*
			vesiculosus	
			acuminatus	*O. ? nathani*

Figure 2.6 Standard left-hand biostratigraphical column developed by the Subcommission on Silurian Stratigraphy (1995).

– *ordovicicus* CBZ boundary is contentious, being located within the latest Caradoc (e.g. Fortey *et al.*, 1995) or within the early Ashgill (e.g. Barnes, 1992). In addition, the taxonomy of the *Amorphognathus* 'plexus' is currently unstable and it is thought that different workers have used different criteria to identify the eponymous biozonal species (Fortey *et al.*, 1995).

The Midcontinent Faunal Region is typically developed on the North American and Siberian cratons, and characterised by low-latitude, warm-water taxa. The conodont biozonal scheme for the Midcontinent has been based on the first appearances of three distinct conodont faunas, informally defined as Faunas 10-12 (Sweet *et al.*, 1971; Figure 2.1), which were widely adopted as a conodont biozonal scheme. Sweet (1984) later developed an alternative to the Fauna 10-12 scheme, using graphical correlation methods, and defined six chronozones (Figure 2.1).

An additional Fauna 13 was proposed by McCracken & Barnes (1981) based upon a distinctive conodont faunal assemblage within the Ellis Bay Formation on Anticosti Island. The base of Fauna 13 is the level in the Ellis Bay Formation where *Gamachignathus ensifer* and *Gamachignathus hastatus* become numerically dominant and so this is an informal acme biozone (McCracken & Barnes, 1981; McCracken & Nowlan, 1986). Although rare elements of *Gamachignathus* have been recovered from other Laurentian-margin sections, they are not sufficiently dominant to identify confidently Fauna 13 anywhere other than Anticosti Island (Amsden & Barrick, 1986; McCracken, 1987; Nowlan *et al.*, 1997). Fauna 13 can only be regarded as a local acme biozone, which may be partially coincident with Fauna 12 (Sweet, 1984).

North Atlantic and American Midcontinent conodont biozonal schemes can be conflated due to the migration of taxa between the regions (Sweet *et al.*, 1971; Sweet, 1984). The base of Fauna 10 is coincident with the base of the *superbus* CBZ (as recognised by Sweet & Bergström, 1984), the bases of Fauna 11 and 12 both occur within the *superbus* CBZ (see Sweet, 1984; Figure 2.1).

The *nathani* CBZ was defined on Anticosti Island by McCracken & Barnes (1981) and spans the Ordovician-Silurian boundary. The top of the biozone was marked by the first appearance of *Distomodus kentuckyensis* (McCracken & Barnes, 1981). The

base of the *nathani* CBZ on Anticosti Island lies within strata bearing conodonts indicative of Fauna 12 / *ordovicicus* CBZ. The fact that the *nathani* CBZ has not been recognised conclusively outside eastern North America, led Aldridge & Schönlaub (1989) to suggest that it is merely a local sub-biozone. In fact, the base of the biozone is not easily recognised even on Anticosti Island due to the low abundance of the nominate species (see Barnes, 1988). Therefore, the *nathani* CBZ is regarded as a local sub-biozone of Fauna 12 within this thesis.

The term *nathani* CBZ has also been used to describe strata which yield a 'transitional fauna' containing conodonts indicative of Fauna 12 / *ordovicicus* CBZ and the *kentuckyensis* CBZ, below the first appearance of *Distomodus kentuckyensis* itself. For example, Melchin *et al.* (1991) recovered a 'transitional fauna' in the Cornwallis Island section which they referred to as the *nathani* CBZ, even though *Oulodus*? *nathani* has not been recovered. It is proposed here that the uppermost Ordovician to lowest Silurian strata yielding a transitional fauna should be informally referred to as a Transitional CBZ and not the *nathani* CBZ.

The development of a standard conodont biozonal scheme for the overlying Silurian strata was initiated by Walliser (1962, 1964, 1972), following observations at Mount Cellon in the Carnic Alps (Austria). He identified Bereich I, *celloni* and *amorphognathoides* CBZs within the Llandovery to Lower Wenlock strata. Alternative biozonal schemes were suggested by Nicoll & Rexroad (1969), Aldridge (1972) and Uyeno & Barnes (1983; Figure 2.7). Aldridge & Schönlaub (1989) revised the biozonal scheme of Walliser (1964) and erected a global standard Silurian scheme (standard scheme utilised herein) based on the first appearances of *Distomodus kentuckyensis*, *Distomodus staurognathoides*, *Pterospathodus celloni* and *Pterospathodus amorphognathoides* (Figure 2.7). They also included a widespread *tenuis* Sub-biozone within the upper *kentuckyensis* CBZ. The base of which is defined by the first appearance of *Pranognathus tenuis*.

The *tenuis* Sub-biozone was placed within the upper *kentuckyensis* CBZ, as it was found associated with elements of the *kentuckyensis* CBZ in the Welsh Borderlands (Aldridge, 1972), Severnaya Zemlya (Männik, 1983) and Niagara Falls (Cooper, 1977). However, in those sections the appearance of *Pranognathus* has now been

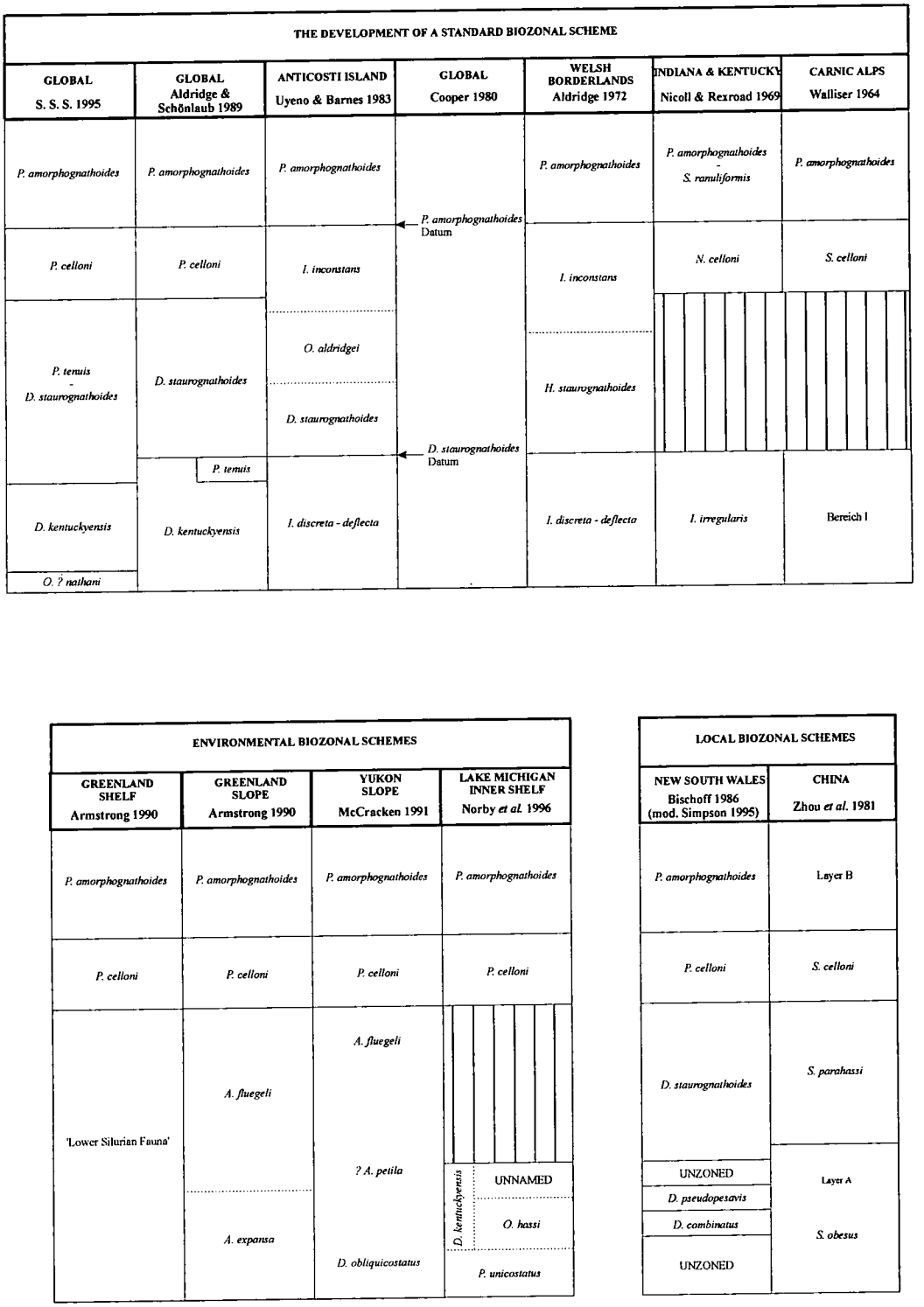


Figure 2.7 Conodont biozonal schemes for the Llandovery. Dashed horizontal lines indicate uncertainty surrounding the exact position of the biozonal boundary Vertical lines represent missing strata.

shown to correlate with the first appearance of *Distomodus staurognathoides* (e.g. Aldridge *et al.* 1993b). The fact that *Pranognathus* and elements of the *kentuckyensis* CBZ co-occur in some sections suggests that elements of the *kentuckyensis* CBZ continued to exist during the basal *staurognathoides* CBZ. In fact, *Distomodus staurognathoides* has been recovered from samples containing conodonts indicative of the *kentuckyensis* CBZ within the basal part of the Brassfield Limestone in the Michigan Basin (Nicoll & Rexroad, 1969, Cooper, 1980). The *tenuis* Sub-biozone is currently regarded as coincident with the base of the *staurognathoides* CBZ rather than occurring within the upper *kentuckyensis* CBZ.

The Aldridge & Schönlaub scheme has proven largely successful as a standard biozonal scheme for the Llandovery and will be referred to as the standard scheme throughout this thesis. However, it has been demonstrated that conodont faunas were largely facies related and varied between shelf and basinal settings (e.g. Aldridge & Mabillard, 1981; Le Fèvre *et al.*, 1976). In pre-*celloni* CBZ successions, the index taxa used in the Aldridge & Schönlaub scheme commonly only occur in shelf environments. This has led to a number of alternative biozonal schemes being erected for deep-water and shallow-water strata (Figure 2.7).

A biozonal scheme for slope sections in Northern Greenland was developed by Armstrong (1990); this comprised the *Pseudolonchodina expansa* and *Pseudolonchodina fluegeli* first appearance biozones (Figure 2.7). The base of the *expansa* and *fluegeli* CBZs were close to the Ordovician-Silurian boundary and within the lower Aeronian respectively, both within the *kentuckyensis* CBZ (Armstrong, 1990). *Pseudolonchodina expansa* and *Pseudolonchodina fluegeli* were also recorded from basinal rocks in the northern Yukon Territories, which lacked the pre-*celloni* CBZ index taxa of the standard scheme (McCracken, 1991b). However, the *expansa* CBZ could not be recognised in that section, as the first appearance of *Pseudolonchodina expansa* occurred in a sample that also contained *Pseudolonchodina fluegeli.* Additionally, McCracken (1991b) erected a first appearance *Dapsilodus obliquicostatus* CBZ for the earliest Llandovery strata.

Herein, *Pseudolonchodina expansa* and *Pseudolonchodina fluegeli* appear in the same horizon within basal Rhuddanian sediments of the shelf-edge section at Prongs Creek

(Yukon Territories). They appear in association with the first appearance of *Distomodus kentuckyensis*. Therefore the Armstrong (1990) biozonal scheme has not proven applicable to other deep-water sections and the pattern observed in Greenland may be a local phenomenon.

Norby *et al.* (1996) studied conodont faunas from shallow-water sections in the Lake Michigan area (Figure 2.7). The *Panderodus unicostatus* CBZ was erected for strata at the base of the Silurian, which lacked any other diagnostic taxa. He also suggested that it would be more applicable to subdivide the *kentuckyensis* CBZ into the *Ozarkodina hassi* interval and an unnamed interval, lacking the index elements of the *Ozarkodina hassi* interval. The *staurognathoides* CBZ has not been recorded in very shallow-water sediments of the American Midcontinent (Norby *et al.*, 1996). The *celloni* CBZ and the *amorphognathoides* CBZ could be identified in the shallow-water sections.

Provincialism within the Lower Silurian has also restricted the global applicability of the standard scheme. Local conodont biozonal schemes have been developed for Silurian strata in Australia and China. Bischoff (1986) identified a large number of species from sections in New South Wales (Australia) that had not been previously identified from other areas and subsequently created a conodont biozonal scheme largely based on the appearance and co-occurrence of the endemic species. This scheme has been correlated with the standard scheme by Simpson (1995). The identification of new species within Chinese sections has also led to the development of a local biozonal scheme (Zhou *et al.*, 1981).

Despite the local and environmental differences discussed above, the Aldridge & Schönlaub (1989) scheme has proven useful as a standard biozonal scheme and has been widely used in the literature. However, the conodont biozonal scheme preferred by the Subcommission on Silurian Stratigraphy (1995) differs from that of the standard scheme in including a *nathani* CBZ and a combined *tenuis* - *staurognathoides* CBZ (Figure 2.6). As has been discussed above, the *nathani* CBZ cannot be identified globally and so should not be included in a standard, global, biozonal scheme. The *tenuis* Sub-biozone has proven a useful division of the basal *staurognathoides* CBZ, and so it seems more advantageous to retain two separate

biozones, rather than combining them into a *tenuis – staurognathoides* CBZ. Therefore, the standard scheme of Aldridge & Schönlaub (1989) is preferred herein to the standard scheme produced by the Subcommission on Silurian Stratigraphy (1995).

2.3.3 Brachiopod Faunas of the Upper Ordovician – Lower Silurian

The *Hirnantia* Brachiopod Fauna has been used to recognise the Hirnantian globally and has been identified on every continent, except for Antarctica (Rong & Harper, 1988). It includes species of *Dalmanella*, *Hirnantia*, *Kinnella*, *Paromalomena*, *Eostropheodonta* / *Apanomena*, *Cliftonia*, *Plectothyrella* and *Hindella* (Rong & Harper, 1988). It has been considered to be cosmopolitan; however, variations do occur: typical *Hirnantia*, atypical *Hirnantia* and Lower Edgewood Faunas, occur within the Kosov (subtropical and temperate latitudes), Bani (marginal to the Gondwanan ice sheets), and Edgewood Provinces (tropical latitudes), respectively (Rong & Harper, 1988).

The relationship between the *Hirnantia* Fauna and the standard graptolite biozonation is uncertain. In Chinese sections, which bear graptolites and brachiopods, the appearance of the *Hirnantia* Fauna is diachronous (Rong, 1984; Figure 2.8). Strata bearing the *Hirnantia* Fauna diachronously overlie sediments of the *mirus*, *uniformis* and *bohemicus* GBZs (Rong, 1984). In all Chinese sections, the extinction of the *Hirnantia* Fauna occurred below strata bearing graptolites of the *persculptus* GBZ (Rong, 1984), thus, implying that the *Hirnantia* Fauna only ranged from within the *pacificus* GBZ to the *extraordinarius* GBZ. However, the *Hirnantia* Fauna has now been recorded within the *persculptus* GBZ in Kazakhstan and Britain (Owen *et al.*, 1991; Owen & Robertson, 1995). The *Hirnantia* Fauna has only been directly found with *Normalograptus extraordinarius* in Kazakhstan, where it is associated with both the *extraordinarius* and *bohemicus* GBZs (Rong & Harper, 1988). The confusion surrounding the correlation of the *bohemicus* and *extraordinarius* GBZs (see Section 2.3.1), and the lack of detailed biostratigraphical and sedimentological analysis through sections containing the *Hirnantia* Fauna, makes it impossible to determine currently the exact relationship between the *Hirnantia* Fauna and the graptolite biozonal scheme. The maximum possible range of the *Hirnantia* Fauna is from the

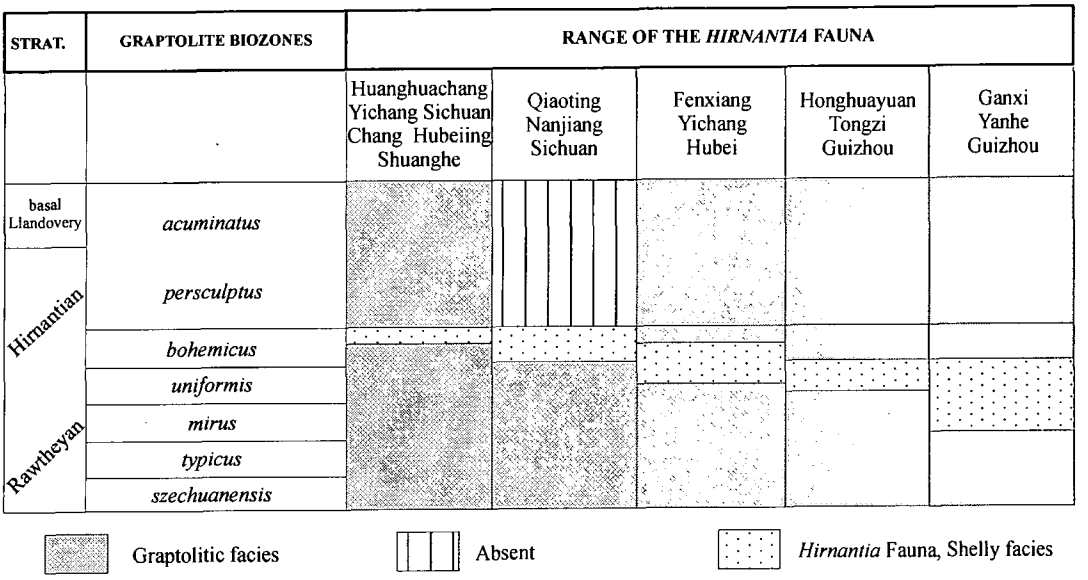


Figure 2.8 The diachroneity of the *Hirnantia* Fauna. From Rong (1984).

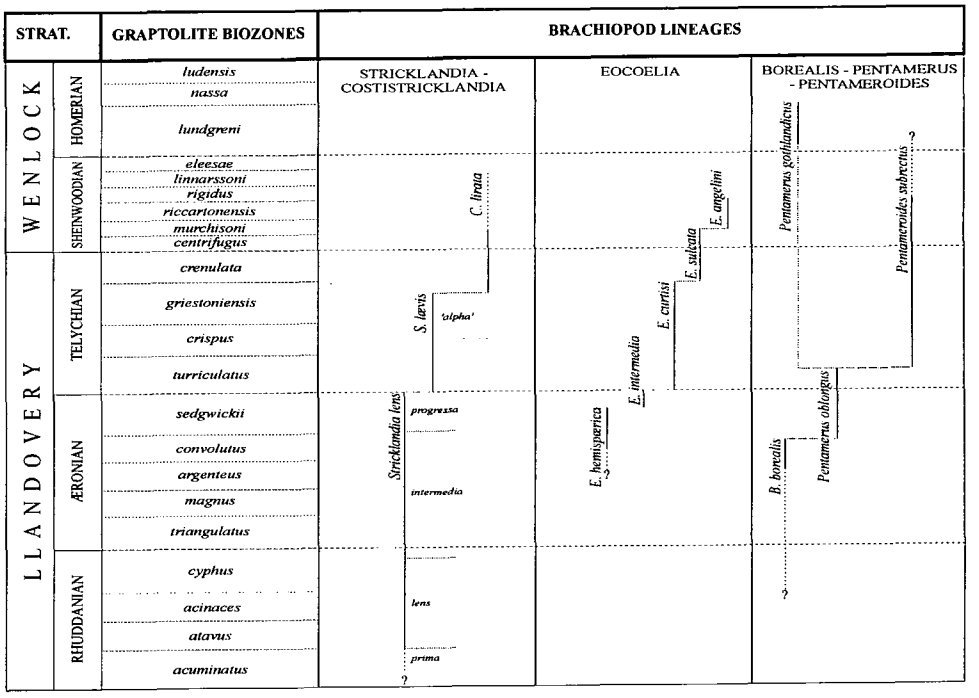


Figure 2.9 Evolving brachiopod lineages through the Llandovery and Wenlock. From Bassett (1989).

pacificus to *persculptus* GBZs, but its appearance and disappearance may be diachronous.

Correlation of Rhuddanian strata using brachiopods is hampered by provinciality, with two distinct provinces occurring: the *Virgiana* (Laurentia, Siberia and Kazakhstan) and *Borealis* (Siberia, Kazakhstan, Baltica and South China) Provinces. During the Aeronian, provinciality broke down and *Pentamerus*, *Stricklandia* and *Clorinda* became widespread, occurring in most tropical and subtropical palaeocontinents (Jin *et al.*, 1996), and are particularly useful in defining depth related shelf communities (e.g. Johnson, 1987).

Correlation of Silurian strata using brachiopods is mainly based on evolving lineages of *Virgiana / Borealis - Pentameroides*, *Eocoelia* and *Stricklandia-Costistricklandia* (Bassett, 1989b; Figure 2.9). Species within the *Pentamerus* and *Pentameroides* lineage have proven useful for correlation. However, the first appearance of *Pentameroides* may be diachronous. Its first appearance has been recorded within the lower Telychian (Bassett, 1989b; Figure 2.9) or the upper Telychian (Johnson *et al.*, 1991b). For example, on Anticosti Island (mid-shelf) it occurs within strata of lower Telychian age (Copper & Jin 1995; Figure 3.19), whereas in the Lake Timiskaming section (inner-shelf), it occurs in upper Telychian strata (evidence herein; Colville & Johnson, 1982). Consequently, the first appearance of *Pentameroides* is diachronous and is not a reliable correlation datum.

2.3.4 A Biostatigraphic Framework: Conflation of the graptolite, brachiopod and conodont biozonal schemes

Correlation of Upper Ordovician and Lower Silurian rocks has been traditionally hampered by the inability to relate directly the graptolite, conodont and brachiopod biozonal schemes. Improving the correlation of the biozonal schemes has been regarded as a priority for researchers (Loydell, 1998). A framework has been developed herein based on current direct and indirect evidence regarding the interrelationships between biozonal schemes (Figure 2.12).

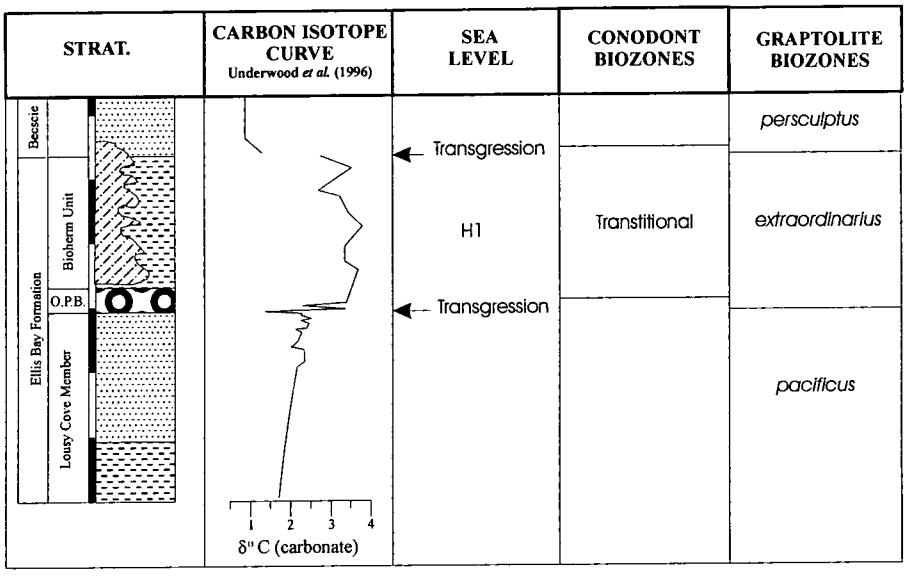


Figure 2.10 A summary of the oxygen and carbon isotope data, sea-level interpretation, conodont biozones and graptolite biozones through the uppermost Ordovician to Lower Silurian strata on Anticosti Island.

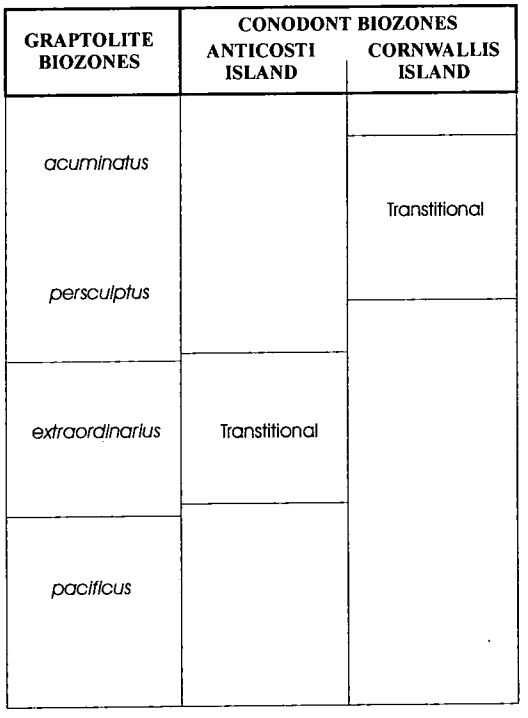


Figure 2.11 A comparison of the correlation of the Transitional CBZ and graptolite biozones in the Anticosti Island and Cornwallis Island sections.

The correlation of conodont and graptolite biozones in the uppermost Ordovician to basal Silurian has been possible on Cornwallis Island (Canadian Arctic) where sections have yielded both graptolites and conodonts (Melchin *et al.*, 1991; Figure 2.3). The graptolite succession includes the *pacificus*, *bohemicus*, *persculptus* and *acuminatus* GBZs. The *bohemicus* GBZ was regarded as being equivalent to the *extraordinarius* GBZ (e.g. Melchin *et al.*, 1991), until the study of Štorch & Loydell (1996), which synonymised *Glyptograptus bohemicus* with *Normalograptus persculptus* (Section 2.3.1). This study suggests that the siltstone within the Cornwallis Island section bearing '*Glyptograptus bohemicus*' was deposited during the *persculptus* GBZ. This would indicate that the siltstone was deposited during the post-glacial transgression rather than the glacial maximum. However, the sea-level interpretation of the section indicates that the siltstone represents the shallowest part of the section. Therefore, it seems more likely to correlate with the glacial maximum and the *extraordinarius* GBZ, than during the *persculptus* GBZ and the post-glacial transgression. Herein, the siltstone bearing '*Glyptograptus bohemicus*' in the Cornwallis Island section is regarded as correlating with the glacial maximum and the *extraordinarius* GBZ.

Within the section, the upper part of the *ordovicicus* CBZ is correlated with the *pacificus* to lower *persculptus* GBZs. The base of the '*nathani*' CBZ *sensu* Melchin *et al.* (1991) (Transitional CBZ, herein) is correlated with the middle of the *persculptus* GBZ and the base of the *kentuckyensis* CBZ correlates with the lower *acuminatus* GBZ (Melchin *et al.*, 1991). The data from Cornwallis Island suggests that the Transitional CBZ ranges from the *persculptus* to *acuminatus* GBZs. However, on Anticosti Island (Québec) the Transitional CBZ is thought to correlate with the *extraordinarius* GBZ, as it occurs in association with a positive $\delta^{13}C$ excursion (Underwood *et al.*, 1997; Section 2.5; Figure 2.10). Consequently, the maximum possible range of the Transitional CBZ is from the *extraordinarius* to *acuminatus* GBZs, and it may be diachronous (Figure 2.11).

The correlation of conodonts and graptolites with the *Hirnantia* Fauna has also proved problematic. The correlation of graptolite biozones and the *Hirnantia* Fauna has been discussed above (Section 2.3.3), the latter is generally thought to range between the

pacificus and *persculptus* GBZs. Only a few localities allow correlation of conodonts with the *Hirnantia* Fauna. The *Hirnantia* Fauna occurs with conodonts indicative of the *ordovicicus* CBZ or Fauna 12 within North American and Austrian sections (McCracken & Barnes, 1982; Amsden & Barrick, 1986; Barnes & Bergström, 1988). However, in Sweden a transitional conodont fauna (Transitional CBZ) has been found within the Hirnantian Loka Formation (Bergström & Bergström, 1996). This suggests partial correlation of the Transitional CBZ, with the *Hirnantia* Fauna.

In summary, the graptolite, conodont and brachiopod biozonal schemes across the Ordovician - Silurian boundary have been correlated using the currently available direct and indirect evidence (Figure 2.12). The *Hirnantia* Fauna is generally thought to range between the *pacificus* to *persculptus* GBZs and the upper *ordovicicus* to Transitional CBZs. The maximum possible range of the Transitional CBZ is from the *extraordinarius* to *acuminatus* GBZs, and it may be diachronous (Figure 2.11). A summary of the correlation of conodonts, graptolites and brachiopods in the uppermost Ordovician is shown in Figure 2.12.

Indirect correlation of graptolites, conodonts and brachiopods through the Llandovery was attempted by Johnson (1987, fig. 5) and later updated by Johnson *et al.* (1991b, fig. 3). Johnson (1987) developed a standard correlation scheme using the graptolite and conodont data from the Welsh Borderlands (Cocks *et al.*, 1984; Aldridge, 1972), plus brachiopod data from Europe and North America (see references therein). The British graptolite biozonal scheme lacks a number of biozones that are currently included within the standard graptolite biozonal scheme (Section 2.3.1; Figure 2.5). However, the two schemes can now be correlated using the studies of Rickards (1995) and Loydell (1993; Figure 2.5).

Johnson *et al.* (1991b) depicted the base of the *staurognathoides* CBZ within the *sedgwickii* GBZ, as in the Welsh Borderlands *Distomodus staurognathoides* was first recorded from within the *sedgwickii* GBZ (Aldridge, 1972). However, there is now indirect evidence to suggest that it occurred earlier. On Anticosti Island (Québec), it first appears in strata bearing graptolites indicative of the upper *acinaces* GBZ to *convolutus* GBZ (Loydell, *pers. comm.*). Additionally, in the Oslo Graben (Norway), *Distomodus staurognathoides* has been recovered from the upper Solvik Formation,

which correlates with the *convolutus* GBZ (Worsley, 1989). It has also been shown that the base of the *tenuis* Sub-biozone correlates with the *convolutus* GBZ (Aldridge, 1975).

Johnson *et al.* (1991b) depicted the base of the *celloni* CBZ within the *turriculatus* GBZ. Direct correlation of conodont and graptolite biozones in the Canadian Cordillera also suggested that the base of the *celloni* CBZ occurs within the *turriculatus* GBZ (McCracken 1991b). However, in that study the *turriculatus* GBZ was not sub-divided into the *guerichi* and *turriculatus* - *crispus* GBZs, as in the current standard graptolite biozonal scheme. The first appearance of *Pterospathodus celloni* in the middle of the combined *turriculatus* GBZ in the Canadian Cordillera may indicate that it first appears near the boundary between the *guerichi* and *turriculatus* - *crispus* GBZs, but more evidence is needed. In a number of shelf sections, *Aulacognathus bullatus* occurs prior to the appearance of *Pterospathodus celloni*. On Anticosti Island, it occurs in association with *Eocoelia curtisi,* indicating correlation with the *guerichi* GBZ.

The base of the *amorphognathoides* CBZ was regarded as occurring within the *crenulata* GBZ by Johnson *et al.* (1991b). The *crenulata* GBZ of the British graptolite scheme (Cocks *et al.*, 1984) is equivalent to three biozones (upper part of the *griestoniensis* - *crenulata* GBZ, *spiralis*, *lapworthi-insectus* GBZs) of the current standard graptolite biozonal scheme (Subcommission on Silurian Stratigraphy, 1995). Direct correlation of the conodont and graptolite biozonal schemes in the Canadian Cordillera indicates that the base of the *amorphognathoides* CBZ actually occurs within the *spiralis* GBZ (McCracken, 1991b, c).

In summary, a biostratigraphic framework for the Upper Ordovician to Lower Silurian has been developed herein (Figure 2.12) by combining and comparing biozonal schemes for conodonts graptolites and brachiopods. This detailed and up-to-date biostratigraphic framework further allows the correlation of chemostratigraphic and sea-level data and will ultimately lead to the development of an 'event' framework for the uppermost Ordovician to early Silurian.

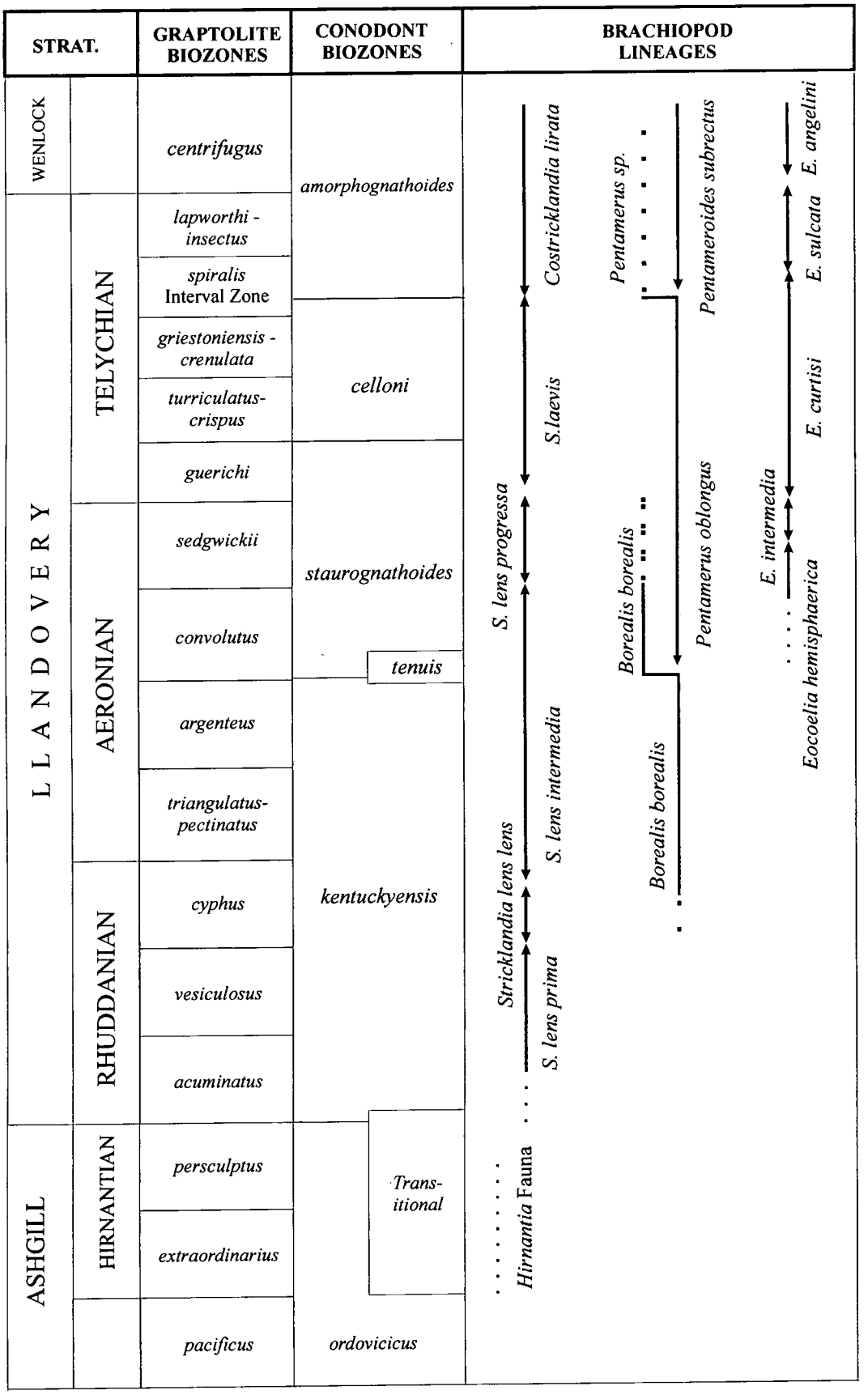


Figure 2.12 Correlation of graptolite and conodont biozones through the Upper Ordovician and basal Silurian strata on Cornwallis Island. After Melchin *et al.* (1991).

2.4 Sea-level cycles

Sea-level cycles have been identified within Upper Ordovician and Lower Silurian strata on a regional and global basis. Cycles are identified by variations in lithofacies and / or biofacies. The biofacies utilised are commonly shelly benthic fossil assemblages, based on the depth-related brachiopod communities of Ziegler (1965). The validity of sea-level curves developed from variations in benthic assemblages has been questioned by a number of authors (e.g. Aldridge *et al.*, 1993b). However, a study by Harris & Sheehan (1996) of sea-level cycles in the eastern Great Basin suggests that sea-level cycles identified by variations in lithology were mirrored by cycles in the brachiopod benthic assemblages, thus suggesting that sea-level cycles identified by variations in benthic assemblages are as valid as those identified using variations in lithology.

2.4.1 Upper Ordovician sea-level cyclicity

Ordovician sea-level curves for North America and Europe (Welsh Basin and Estonia) were constructed from facies and coastal onlap changes by Ross & Ross (1992). Generally, high sea levels prevailed within the Upper Ordovician (Mohawkian and Cincinnatian), with a general fall in sea level indicated towards the end of the Ordovician. Five transgressive-regressive (T-R) cycles occurred within the Cincinnatian (Figure 2.1), with the ultimate cycle being a minor T-R cycle within the Hirnantian (Global Cycle H1). The cycle was identified in strata bearing the *Hirnantia* Fauna in the Illinois Basin (Neda, Noix and Giradeau Formations), Oklahoma (Keel Limestone), and Estonia (uppermost Harju Series) by Ross & Ross (1992). It has also been identified in sea-level curves constructed from Upper Ordovician strata in Iowa (Witzke & Bunker, 1996), the eastern United States (Holland & Patzkowsky, 1996), and the eastern Great Basin (Harris & Sheehan, 1996; Figure 2.13). The top of this minor T - R cycle is marked by a significant unconformity (Ross & Ross, 1992).

In deep-water graptolitic sections, a T-R cycle (H1) would be expected to occur within the *extraordinarius* GBZ. However, the *extraordinarius* GBZ is commonly interpreted as the point of maximum regression (rather than a minor transgressive-

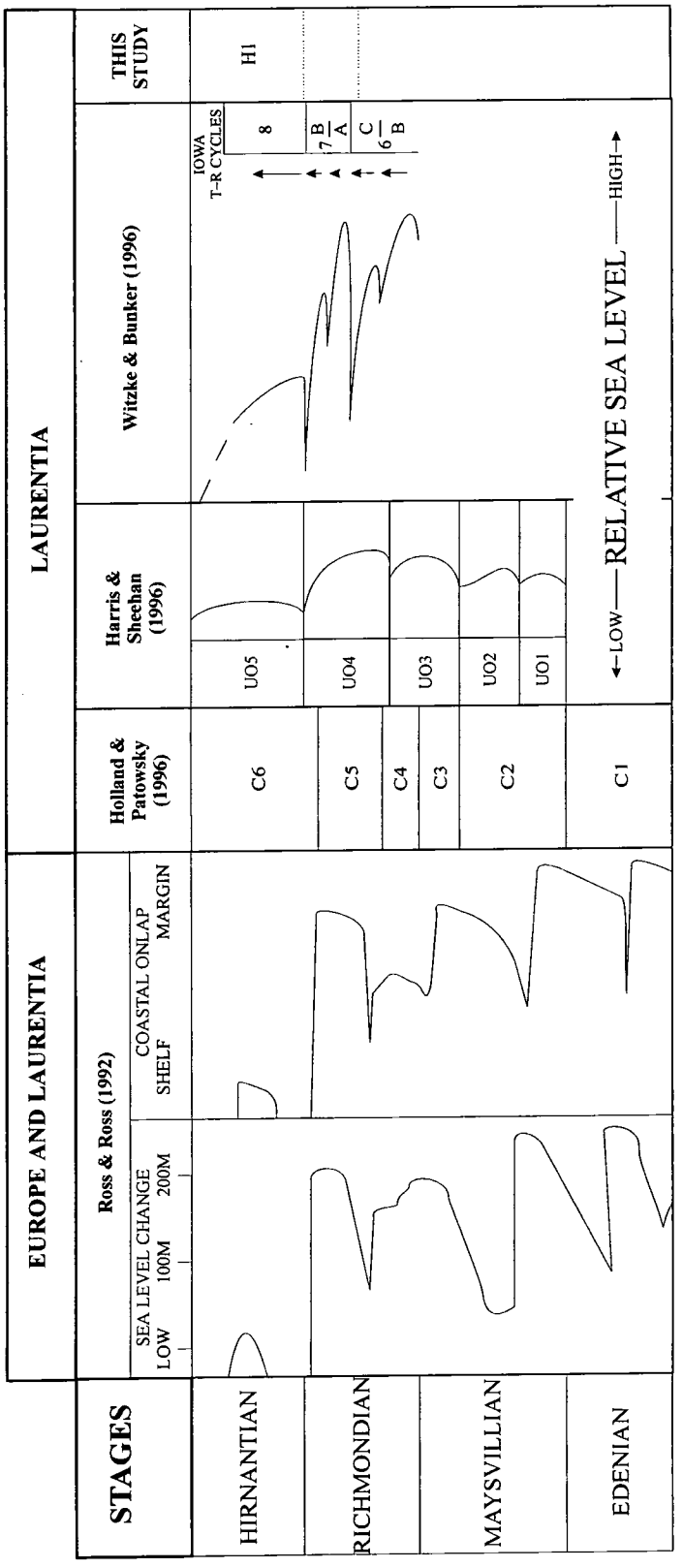


Figure 2.13 The correlation of Upper Ordovician sea-level curves.

regressive cycle), and is followed by the major post-glacial transgression within the *persculptus* and *acuminatus* GBZs (e.g. Wang *et al.*, 1993b; Melchin *et al.*, 1991). Thus, Global Cycle H1 has not been identified in deep-water successions. A possible explanation is that it was a minor sea-level cycle that it had little expression in deep-water successions.

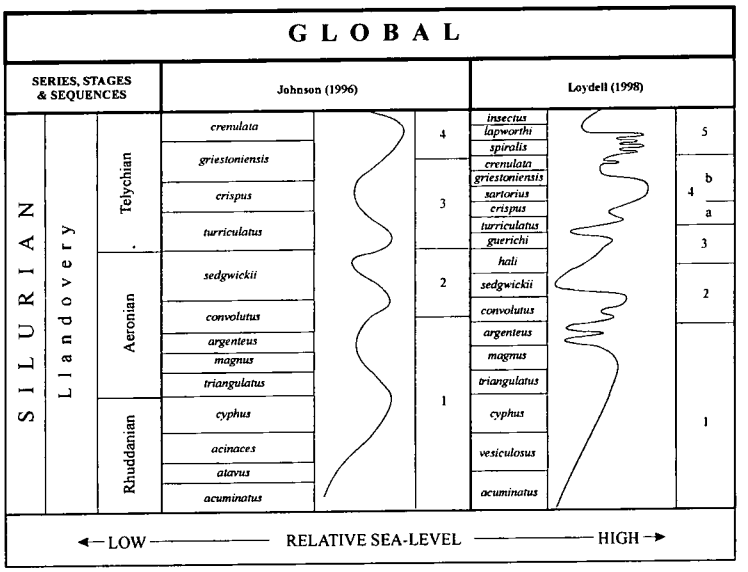
2.4.2 Lower Silurian sea-level cyclicity

2.4.2a Global sea-level cycles

Two global sea-level curves have been constructed through the Llandovery: the Johnson and Loydell Curves (Johnson, 1996; Loydell, 1998). The Johnson Curve was constructed using variations in benthic assemblages in shallow-water successions (Figure 2.14), whilst the Loydell Curve was constructed using lithological and faunal changes in deep-water successions (Figure 2.14).

The Johnson Curve has been revised and its global applicability tested in a number of successive papers (Johnson, 1987; Johnson & McKerrow, 1991; Johnson, 1996). In the initial paper, Johnson (1987) compared the sea-level curves of 22 Laurentian sections. He identified 4 main highstands within the Llandovery, which could be directly dated using brachiopod faunas. The highstands occurred within the Rhuddanian to early Aeronian, late Aeronian, early Telychian and late Telychian, and were marked by the appearance of *Virgiana*, *Stricklandia lens progressa- Eocoelia intermedia*, *Stricklandia laevis-Pentamerus oblongus*, *Eocoelia curtisi* and *Pentameroides suberectus*, respectively.

The highstands could not be directly dated using graptolites, which are rare in the shallow-water successions. However, the occurrence of brachiopods and graptolites in British sections allowed Johnson (1987) to indirectly correlate the brachiopod assemblages with the British graptolite biozonal scheme of Cocks *et al.* (1984). Unfortunately, the British graptolite biozonal scheme differs from the standard graptolite biozonal scheme currently recommended. However, the two schemes can be tentatively correlated using data from the literature (e.g. Loydell, 1993: Rickards,



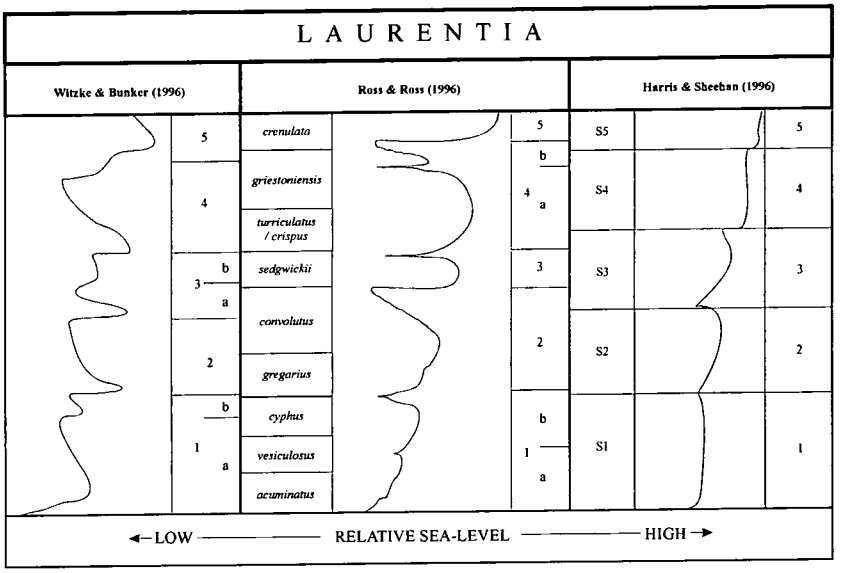


Figure 2.14 Correlation of the global and Laurentian sea-level curves for the Llandovery.

1995; Section 2.3.1; Figure 2.5). In the Johnson & McKerrow (1991) study, the Rhuddanian to early Aeronian highstand was marked by the appearance of *Virgiana*, and was depicted as occurring within the *cyphus* to *triangulatus-pectinatus* GBZs. However, the appearance of *Virgiana* has now been directly correlated with the *cyphus* GBZ (see Jin *et al.*, 1996). Likewise, the late Aeronian highstand, marked by the appearance of *Stricklandia lens progessa* and *Eocoelia intermedia*, was depicted within the *convolutus* to *sedgwickii* GBZs by Johnson & McKerrow (1991, fig.1). However, the appearance of *Stricklandia lens progressa* and *Eocoelia intermedia* actually correlates with the upper *sedgwickii* GBZ rather than the *convolutus* to *sedgwickii* GBZs (Johnson, 1987; Bassett, 1989b). Thus, this highstand is regarded as occurring within the *sedgwckii* GBZ, herein.

The early Telychian highstand coincides with the appearance of *Stricklandia laevis*, *Pentamerus oblongus* and *Eocoelia curtisi*. Johnson (1987) correlated it with the *turriculatus* GBZ, which is divided into the *guerichi* and *turriculatus-crispus* GBZs in the current standard scheme. Johnson & McKerrow (1991) depicted the late Telychian highstand within the *crenulata* GBZ, which is equivalent to the *crenulata*, *spiralis*, *lapworthi* and *insectus* GBZs of the current standard scheme (Figure 2.4 and 2.5).

In order to test the global applicability of his curve, Johnson (1996) compared the sea-level curve for Laurentia (eastern Iowa), with those of Avalonia (Wales & England), Baltica (Saaremaa, Estonia), Bohemia (Prague Basin), Cathaysia (South China) and Gondwana (New South Wales). He suggested that the four Llandovery highstands originally identified on Laurentia could also be identified on the other palaeocontinents studied. Thus, he concluded that the four cycles were global. However, correlation of the strata from the different palaeocontinents is partially incorrect. It has been suggested that the formations within the Chinese section were incorrectly correlated and dated (Loydell, 1998). For example, the base of the lower Telychian *celloni* CBZ in China occurs within the upper Xiushan Formation (Lin, 1983), but this formation is depicted as occurring within the uppermost Telychian by Johnson (1996). This has caused some doubt to be placed on the findings of the Johnson (1996) study.

The global sea-level curve of Loydell (1998) was constructed using lithological and faunal evidence for sea-level change in deep-water sections on Laurentia, Gondwana, Baltica, eastern Avalonia, South China, and Siberia (Figure 2.14). Loydell (1998) identified transgressions by the 'appearance of graptolitic, dark-grey, laminated shales and mudstones' in shelf sections, or condensed sequences in offshore sections. Regressions were recognised by the appearance of 'coarser, turbiditic and / or bioturbated beds' in sections dominated by graptolitic shales. He did not utilise graptoloid diversity changes as evidence for sea - level fluctuations. The cycles identified were directly dated using graptolites and the graptolite biozonal scheme used is that recommended by the Subcommission for Silurian Stratigraphy (1995; Figure 2.14).

Loydell (1998) identified five highstands during the Llandovery, in the early Aeronian, the *convolutus* GBZ, *guerichi* GBZ, late *turriculatus* GBZ, upper *crispus* - lower *griestoniensis* GBZ and *spiralis*-lower *lapworthi* GBZs. With low sea levels during the *argenetus* and *sedgwickii* GBZs, the *utilis* subzone (late *guerichi*-early *turriculatus* GBZs) and *lapworthi* GBZ.

Correlation of the two curves has proven difficult, as the Johnson Curve was directly dated using brachiopods and the Loydell Curve was dated using graptolites. The Johnson Curve was compared to the British graptolite biozonal scheme of Cocks *et al.* (1984) which differs from the standard biozonal scheme utilised by Loydell (1998). However, using the biostratigraphic framework developed herein and data from the literature (e.g. Loydell, 1993), the brachiopod and graptolite biozonal schemes can be correlated. The discussion below aims to compare the two curves and to identify and global sea-level cycles through the Llandovery (Figure 2.15). The global cycles will be consecutively numbered and prefixed with the letter G.

Both of the global curves depict a T-R cycle from the base of the Rhuddanian to Lower Aeronian (G1). Within the mid Aeronian, Loydell (1998) identified transgression at the base of the *convolutus* GBZ in deep-water sections, which had not been identified in the shallow-water study conducted by Johnson (1996). However, six of the 22 sections included in the Johnson (1987) study show a deepening event within the *convolutus* GBZ (five of the sections do not cover this interval). A

transgression also occurs at this point (coincident with the first appearance of *Pentamerus*) in the Iowa section (Witzke & Bunker, 1996), which Johnson (1996) regarded as the 'type section' for the Llandovery. Therefore, there is some evidence from Laurentian sections that a deepening event occurred within the mid Aeronian. In order to determine whether this is a global cycle evidence for it has to be found on other palaeocontinents.

There is some evidence from the literature that deepening did occur in association with the appearance of *Pentamerus* on Baltica (Oslo; Worsley, 1989) and Siberia (Severnaya Zemlya; Männik, 1983). However, the sea-level curves for other palaeocontinents constructed by Johnson (1996), do not indicate that deepening occurred within the *convolutus* GBZ. In summary, there is evidence that a global deepening event did occur in the *convolutus* GBZ, as indicted by the Loydell Curve, even though this was not identified by the Johnson Curve. This is regarded as a global cycle, herein (G2).

The highstand identified within the upper *sedgwickii* GBZ by Johnson (1996) was not depicted in the Loydell Curve. Loydell (1998) depicted a sea-level rise through the *sedgwickii* GBZ. However, he did state that the sea-level evidence was conflicting for the *sedgwickii* GBZ, and that several fluctuations in sea level may have occurred. This has been tentatively included as a global cycle herein (G3).

A major transgression at the base of the Telychian is depicted in both global curves, and can be termed Global Cycle G4. Loydell (1998) identified a sea-level fall between two highstands at the boundary between the *guerichi* and *turriculatus* GBZs (Loydell, 1998), and thus two cycles were identified within Global Cycle G4. These have been termed Global Cycles G4a and G4b, herein. Loydell (1998) depicted the base of Global Cycle G4a within the *guerichi* GBZ, and the base of Global Cycle G4b within the *turriculatus* GBZ. These cycles need to be identified in shallow-shelf sections for their global applicability to be determined. The base of the *guerichi* GBZ represents the base of the Telychian, which in shelf sections is coincident with the appearance of the brachiopods *Eocoelia curtisi* and *Stricklandia laevis*. The section on Anticosti Island provides some evidence that Global Cycle G4b can also be seen in shallow water. A sea-level cycle was identified by Long (1996) within the Pavillion Member

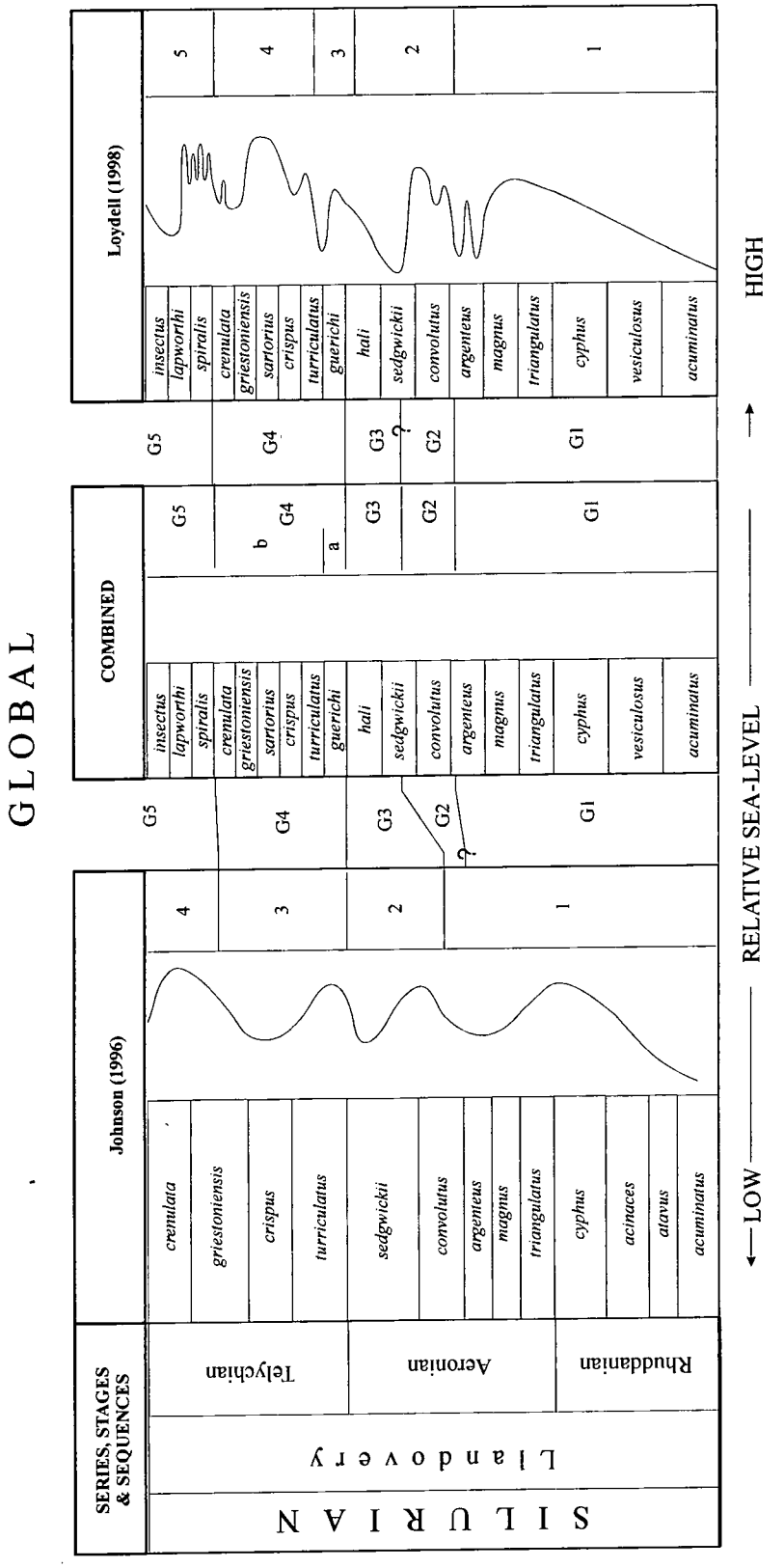


Figure 2.15 Coomparison of the global and sea-level curves for the Llandovery.

of the Jupiter Formation, within which *Eocoelia curtisi* first appears. The base of this cycle occurs just prior to the base of the *celloni* CBZ, and is coincident with the appearance of a distinctive conodont species, *Aulacognathus bullatus*, which may in future prove useful in correlation. Therefore, Global Cycle G4 can be tentatively sub-divided.

A T-R cycle in the upper Telychian is seen in both curves (Cycle 4 of Johnson, 1996 and Cycle 5 of Loydell, 1998; Figure 2.14). The base of this cycle was placed within the *spiralis* GBZ by Loydell (1998), but within the *griestoniensis* GBZ by Johnson (1996). This dichotomy may have resulted from the problems of correlating upper Telychian graptolite biozonal schemes (Section 2.3.1). It is regarded as occurring within the *spiralis* GBZ herein.

In summary, five T-R cycles can be identified within the Llandovery by comparing and refining the global sea-level curves of Johnson (1996) and Loydell (1998). The cycles occur within the Rhuddanian to mid Aeronian (G1), mid Aeronian (G2), upper Aeronian (G3), Lower Telychian (G4a, G4b) and the upper Telychian (G5; Figure 2.15).

2.4.2b Laurentian sea-level cycles

This thesis is largely based on data from Laurentian sections, thus it is important to identify the global cycles in Laurentian sections and to determine whether any additional local cycles occur. The global cycles identified above can be compared with a number of local sea-level curves that have been developed for sections on the North American Craton. Cycles identified in Laurentian sections will be numbered consecutively and prefixed with L (Figure 2.16).

Local curves have been constructed using variations in lithology for sections in eastern Iowa (Witzke & Bunker, 1996), the Illinois Basin (Ross & Ross, 1996) and the eastern Great Basin (Harris & Sheehan, 1996; Figure 2.14). The curves can be correlated using stage boundaries (Figure 2.10), and / or the appearance of brachiopod faunas (Figure 2.17). Within the Rhuddanian to the lower Aeronian, three T-R cycles are identified (Laurentian cycle L1a, L1b, and L1c). This is in contrast with the global

sea-level curves, which depict only one cycle within the Rhuddanian to mid Aeronian. Laurentian Cycle L1a extends from the *persculptus* GBZ to the *vesiculosus* GBZ. It is associated with the basal part of the *kentuckyensis* CBZ. Cycle L1b is marked by the appearance of *Virgiana*, which has been directly correlated with the *cyphus* GBZ (see Jin *et al.* 1996), and coincident with highstand 1 of the Johnson Curve. The youngest cycle (L1c) occurs between the *triangulatus-pectinatus* and *argenteus* GBZs, and the upper part of the *kentuckyensis* CBZ.

Within the Mid Aeronian, the base of a T-R cycle has been identified in association with the first appearance of *Pentamerus* in Iowa (Witzke & Bunker, 1996) and the eastern Great Basin (Harris & Sheehan, 1996; L2). The first appearance of *Pentamerus* has been correlated with the *convolutus* GBZ (Figure 2.12) and so this cycle can be directly correlated with Global Cycle G2. This cycle has not been identified in the Illinois Basin (Ross & Ross, 1996).

Within the upper Aeronian, a minor cycle has been identified in Iowa (Witzke & Bunker, 1996) and a major cycle in the Illinois Basin (Ross & Ross, 1996), which has been identified in the eastern Great Basin (Harris & Sheehan, 1996). It is tentatively recorded as a cycle (L3), which may correlate with Global Cycle G3. The basal Telychian is marked by the base of a T-R cycle (L4) in all the curves. Global Cycles G4a and G4b cannot be differentiated in the local sea-level curves. An Upper Telychian T-R cycle occurs in all of the curves (L5), which may be correlated with Global Cycle G5.

In summary, Laurentian cycles have been identified within the lower to mid Rhuddanian (L1a), upper Rhuddanian (L1b), basal Aeronian (L1c), mid Aeronian (L2), upper Aeronian (L3), lower Telychian (L4) and the upper Telychian (L5; Figure 2.16). The Laurentian cycles differ from the global cycles discussed above in that more than one cycle occurs within the Rhuddanian to mid-Aeronian (L1a-c=G1). The Laurentian cycles in the mid Aeronian (L2=G2), upper Aeronian (L3=G3), lower Telychian (L4=G4) and upper Telychian (L5=G5) can be correlated with the global cycles.

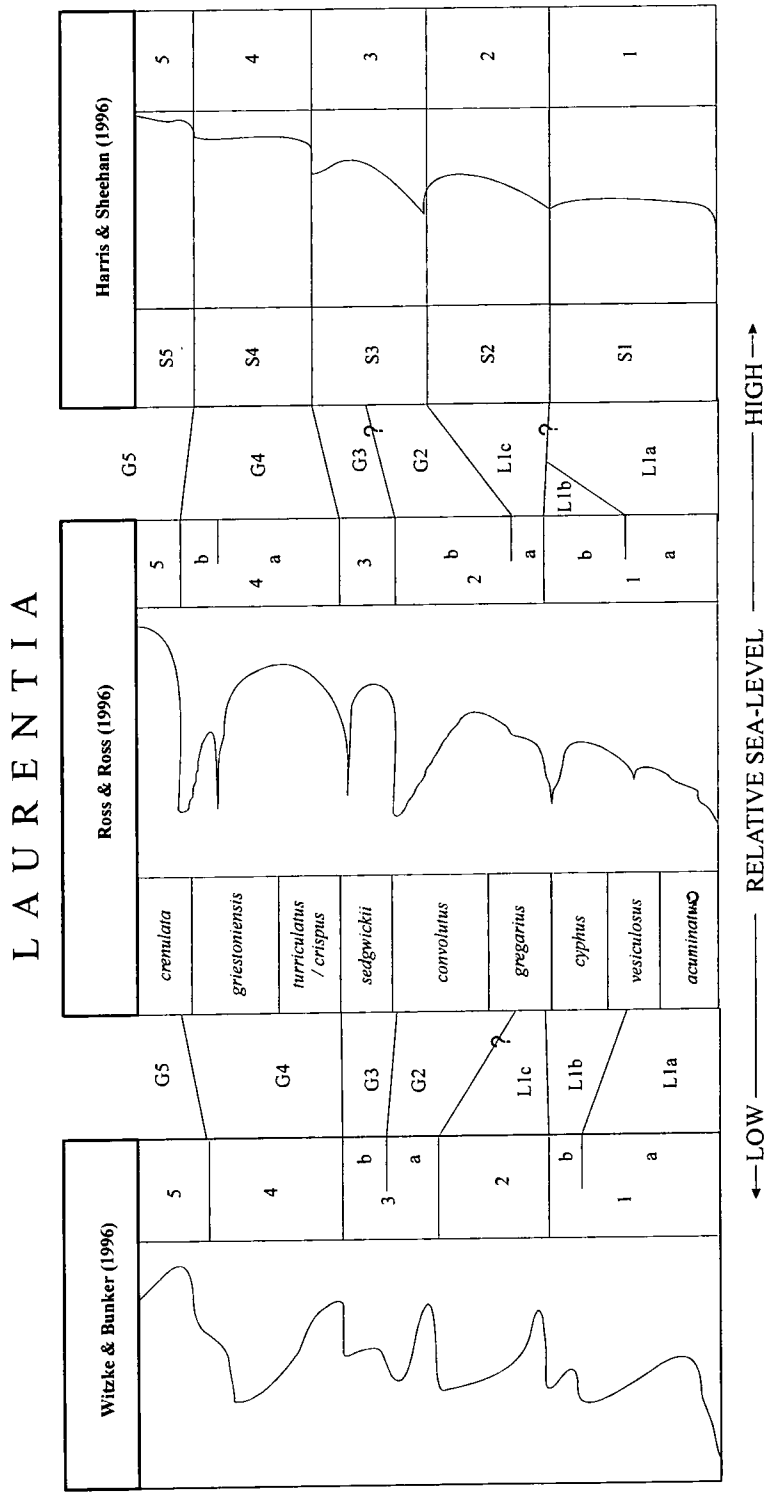


Figure 2.16 Comparison of the Laurentian sea-level curves for the Llandovery.

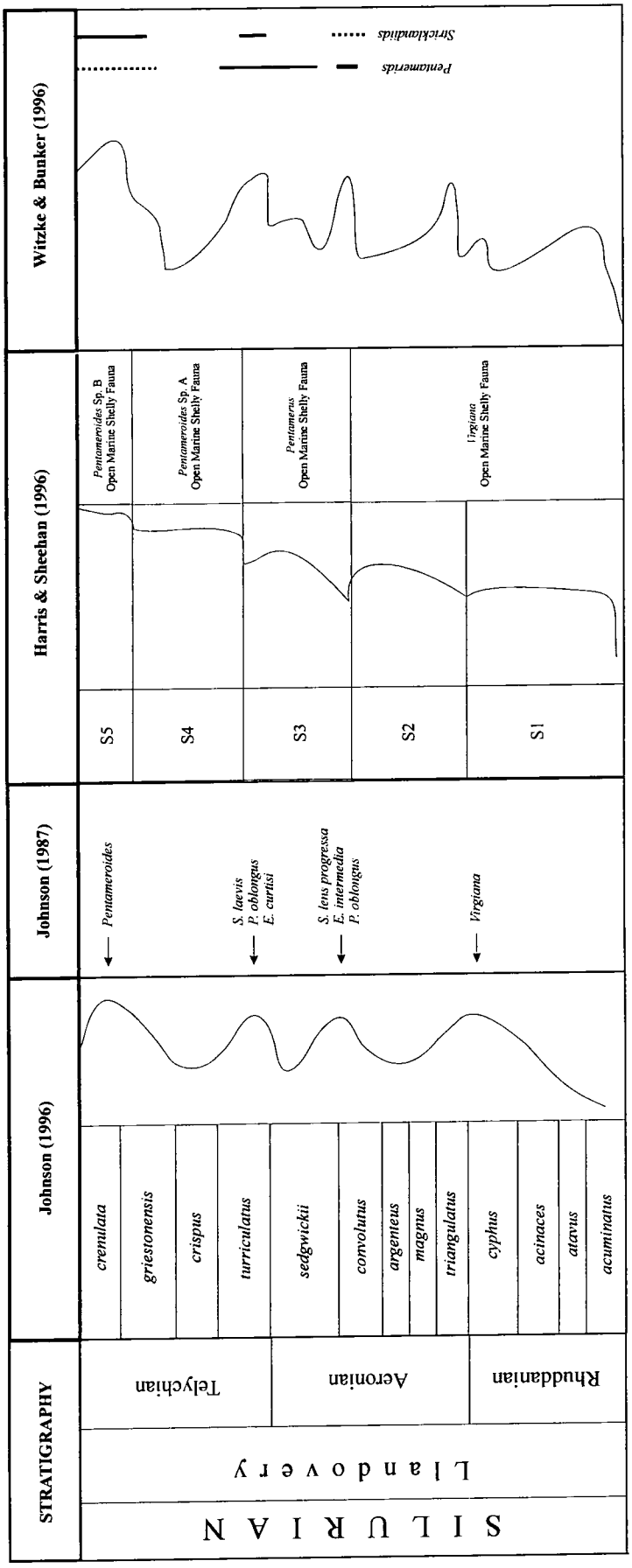


Figure 2.17 Correlation of Laurentian sea-level curves for the Llandovery with brachiopod data.

2.5 Chemostratigraphy

Geochemical studies of Upper Ordovician and Lower Silurian strata have focused on elucidating the climatic events associated with the end-Ordovician mass extinction event, but anomalies are also potentially useful for correlation of Upper Ordovician and Lower Silurian strata.

An Upper Ordovician positive $\delta^{18}O$ excursion, regarded as reflecting glacial cooling and / or an increase in the volume of water stored on land as ice (Marshall & Middleton, 1990; Brenchley *et al.*, 1994; Section 1.7.1), has been recorded from Sweden (Marshall & Middleton, 1990; Figure 2.18), the Baltic States (Brenchley *et al.*, 1994; Marshall *et al.*, 1997; Heath *et al.*, 1998) and Argentina (Marshall *et al.*, 1997). The $\delta^{18}O$ excursion has not been directly correlated with graptolites or conodonts, but can be directly correlated with the *Hirnantia* Fauna in all three areas. The end of the excursion has only been recorded in the Baltic States section where the excursion is thought to cease prior to the upper Hirnantian (*persculptus* GBZ; Brenchley *et al.*, 1994).

It has been generally suggested that the $\delta^{18}O$ excursion correlates with a major glacially induced sea-level fall (e.g. Brenchley *et al.* 1994) and that $\delta^{18}O$ returned to pre-excursion levels during a major post-glacial transgression (Figure 2.18). However, as has been discussed above, the Hirnantian sediments may in fact represent a minor transgression within the major glacial regression (H1; Section 2.4). The excursion occurs between two unconformities in the Baltic States (Heath *et al.*, 1998; Wenzel & Joachimski, 1996) suggesting that it occurs during a time of rising sea level between two regressions.

The $\delta^{18}O$ excursion is found associated with a positive $\delta^{13}C$ excursion. The $\delta^{13}C$ excursion has additionally been recorded in China (Wang *et al.*, 1993a, 1997), Canada (Wang *et al.*, 1993b; Orth *et al.*, 1986; Long, 1993; Brenchley *et al.*, 1994; Underwood *et al.*, 1997), and Scotland (Underwood *et al.*, 1997). It has been interpreted as indicating an increased level of pCO_2 in the ocean (Marshall & Middleton, 1990), a decrease in atmospheric and marine CO_2 (Wang *et al.*, 1993a,

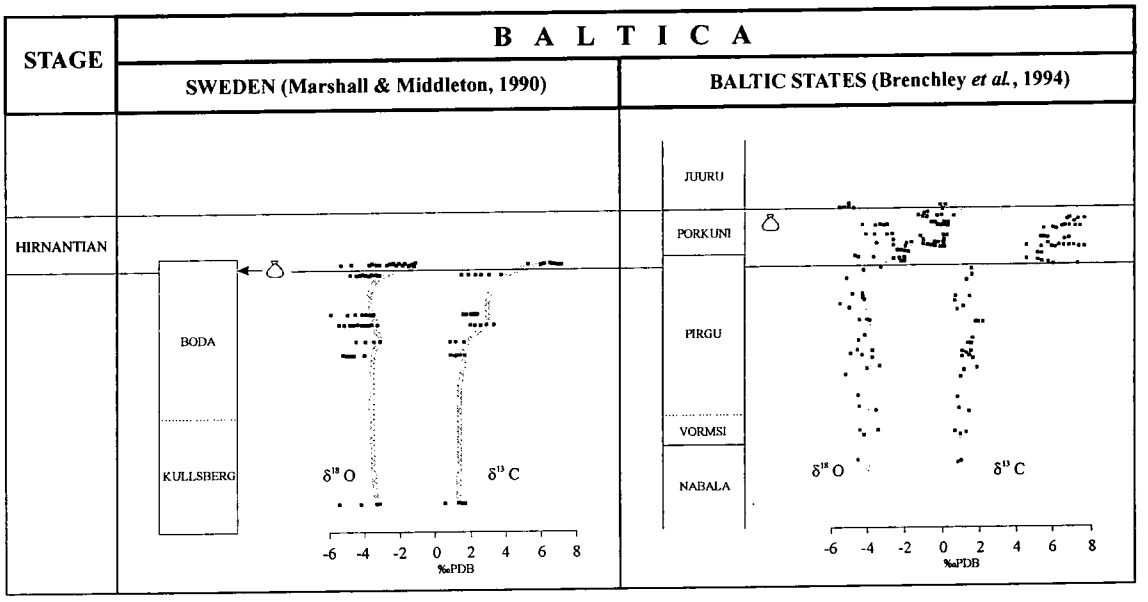
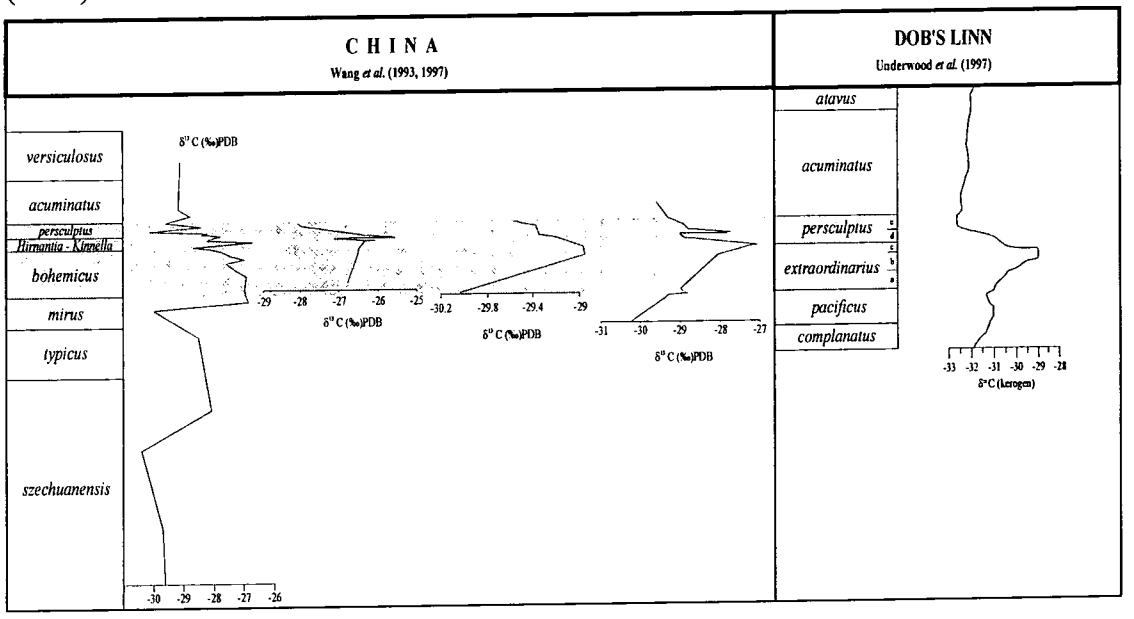


Figure 2.18 Stable oxygen and carbon isotope curves for the Hirnantian. From Marshall & Middleton (1990) and Brenchley *et al.* (1994). The shell symbol indicates the position of the *Hirnantia* Fauna.

Figure 2.19 The positive carbon isotope excursion correlated with graptolite biozones in China and Scotland. China after Wang *et al.* (1993a, 1997). Scotland after Underwood *et al.* (1997).



GRAPTOLITE BIOZONES	BOUNDARIES Pre 1985		Post 1985		BATHYMETRIC CHANGES / ISOTOPIC VALUES
acuminatus	SILURIAN	RHUDDANIAN	SILURIAN	RHUD.	$\delta^{13}C$ = +1 to +3‰
persculptus			ORDOVICIAN	HIRNANTIAN UPPER	$\delta^{18}O$ ~ -4‰
					← SEA LEVEL RISE
extraordinarius / bohemicus	ORDOVICIAN	HIRNANTIAN		HIRNANTIAN LOWER	$\delta^{13}C$ = +4 to +7‰
					$\delta^{18}O$ = -3 to 0‰
					← SEA LEVEL FALL
anceps / pacificus		RAWTHEYAN		RAWTHEYAN	$\delta^{13}C$ = -1 to +3‰
					$\delta^{18}O$ = -3 to -5‰

Figure 2.20 A summary of the Oxygen and Carbon isotope curves through the uppermost Ordovician. From Marshall *et al.* (1997).

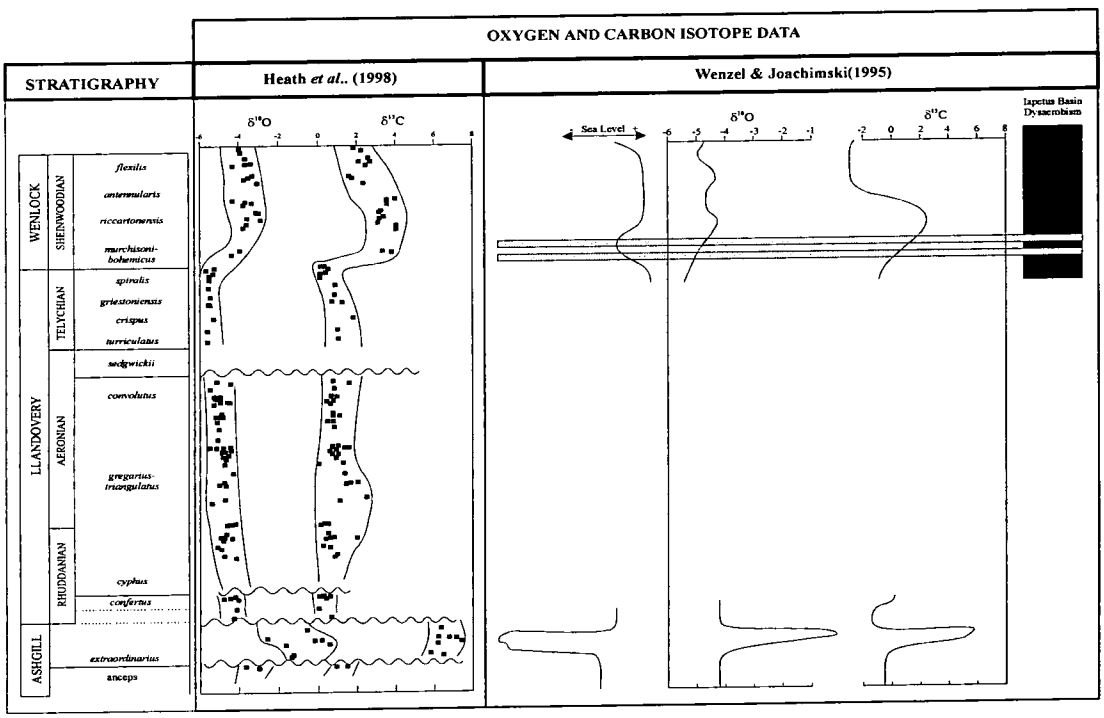


Figure 2.21 Oxygen and Carbon isotope curves for the Ashgill to Wenlock from Gotland (Wenzel & Joachimski, 1995) and Estonia (Heath *et al.*, 1998).

1997) and an increase in organic carbon burial or bioproductivity (Wang *et al.*, 1993b; Brenchley *et al.*, 1994; Marshall *et al.*, 1997). In the Avalanche Lake (North West Territories) section, two positive $\delta^{13}C$ excursions occurred, separated by a sharp negative $\delta^{13}C$ excursion (Wang *et al.*, 1993b; Figure 2.22). The positive $\delta^{13}C$ excursions have been interpreted as indicating increased bioproductivity and the $\delta^{13}C$ negative excursion as a biomass reduction coincident with mass extinction (Wang *et al.*, 1993b).

Determining the exact relationship of the excursion with the graptolite, conodont and brachiopod biozonal schemes has been difficult. In the shelf successions of Sweden, the Baltic States and Argentina, the $\delta^{13}C$ excursion can be directly correlated with the *Hirnantia* Fauna. Correlation with the graptolitic biozonal scheme is possible in the Dob's Linn section (Scotland) and Chinese sections. At Dob's Linn, the $\delta^{13}C$ ratio peaks within the upper *extraordinarius* GBZ and falls rapidly within the *persculptus* GBZ (Underwood *et al.*, 1997; Figure 2.19). In China, the excursion varies between sections, but generally occurs within the upper *mirus* (=*pacificus*) to basal *persculptus* GBZs (Wang *et al.*, 1993a, 1997: Figure 2.19).

Correlation of the excursion with the conodont biozonal scheme is enabled by sections on Anticosti Island and Avalanche Lake. On Anticosti Island, the positive $\delta^{13}C$ excursion occurs in association with the Transitional CBZ, but in the Cornwallis Island section it is associated with taxa indicative of the Fauna 12 (Nowlan *et al.*, 1988; Wang *et al.*, 1993b). Therefore, the excursion may correlate with the upper part of Fauna 12 and / or the Transitional CBZ.

It has been suggested that the $\delta^{13}C$ excursion correlates with the major-glacial regression (Brenchley *et al.*, 1994; 1995; Figure 2.20). In the Avalanche Lake section, the initial positive $\delta^{13}C$ excursion occurs within the bed which has been interpreted to mark the shallowest part of the succession (Wang *et al.*, 1993b). However, evidence from the Anticosti Island sections suggests that the excursion correlates with a minor transgressive - regressive cycle, which occurred at a time of low sea level (H1; Section 3.3.3). Thus, results are currently inconclusive regarding the correlation of the $\delta^{13}C$ excursion and sea-level fluctuations.

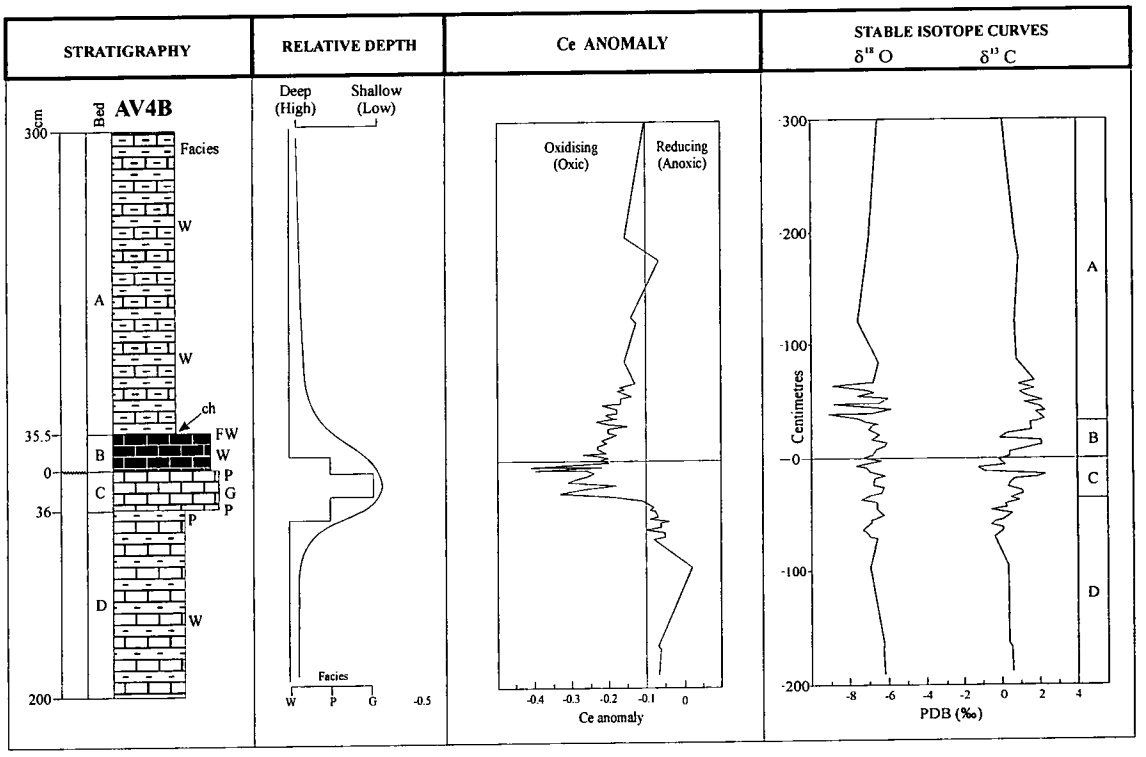
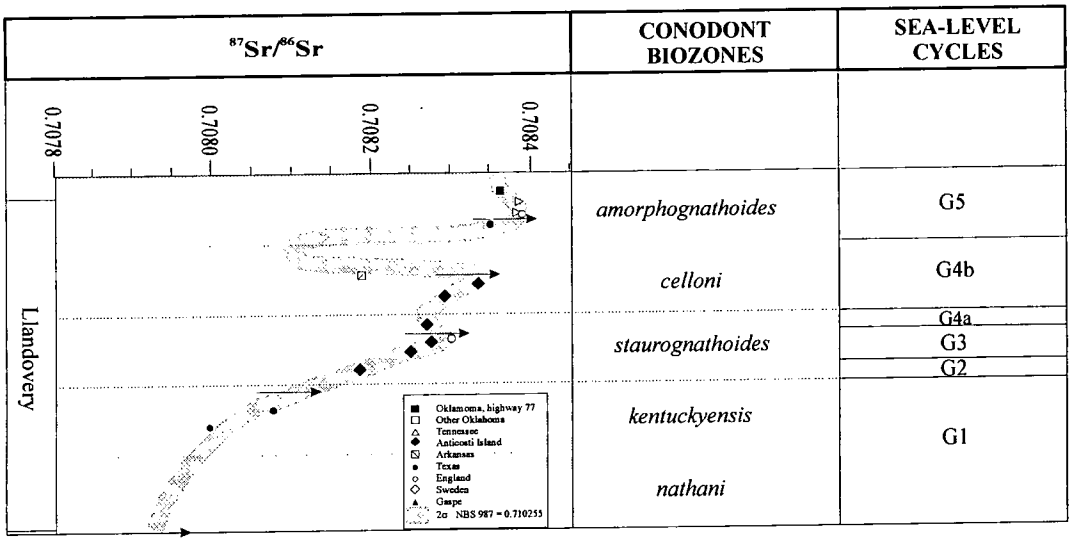


Figure 2.22 Lithological, sea-level and geochemical variations through the Avalanche Lake section. After Wang *et al.* (1993b). Beda D-A are within the Whittaker Formation. Symbols for microfacies: W, wackstone; P, packstone; G, peloidal grainstone; FW, floatstone in a wackestone matrix; ch, condensed horizon.

Figure 2.23 $^{87}Sr/^{86}Sr$ trend through the Silurian. From Ruppel *et al.* (1996).



In summary, the $\delta^{18}O$ and $\delta^{13}C$ excursions can be directly correlated with the *Hirnantia* Fauna. Direct correlation of the $\delta^{13}C$ excursion and the graptolitic biozonal scheme indicates that the $\delta^{13}C$ excursion occurred between the upper *extraordinarius* and *persculptus* GBZs. The $\delta^{13}C$ excursion occurs in sediments bearing conodonts indicative of Fauna 12 and/or the Transitional CBZ. The $\delta^{18}O$ and $\delta^{13}C$ excursions occurred at a time of generally low sea level, but during a minor transgressive - regressive cycle (H 1).

Other geochemical studies across the Ordovician – Silurian boundary have identified variations in Cerium (Ce), Sulphur ($\delta^{34}S$) and Iridium (Ir). A negative Cerium (Ce) excursion has been recorded in association with the positive $\delta^{13}C$ excursion at Avalanche Lake (Wang *et al.*, 1993b). The excursion occurs within the shallowest-water bed and extends into the *persculptus* GBZ (Wang *et al.*, 1993b; Figure 2.19). Negative Ce anomalies from fossil and whole rock samples have been suggested to indicate oxygenation of the water from which the fossil or rock formed. However, the relationship between Ce anomalies and red-ox conditions is not yet clear (Holser, 1997). The Upper Ordovician excursion has been interpreted as representing a period of oxygenated bottom waters, and thus the initiation of thermo-haline circulation. Ce has only been studied in one Upper Ordovician section and so its potential use as a correlation tool is yet unknown.

A study of the $\delta^{34}S$ ratio through the uppermost Ordovician and Lower Silurian has identified a sudden increase in $\delta^{34}S$ at a horizon no older than the base of the *persculptus* GBZ in the Selwyn Basin (northwest Canada; Goodfellow *et al.* (1992). Increases in $\delta^{34}S$ have been interpreted as episodes of anoxic bottom water formation (see Strauss, 1997). The excursion in the *persculptus* GBZ has been interpreted as representing an inversion of stratified ocean water and the cessation of the glacial maximum.

Iridium (Ir) excursions have been detected near to the base of the *persculptus* GBZ in north-western Canada, (Goodfellow *et al.*, 1992; Wang *et al.*, 1993b), eastern Canada (Orth *et al.*, 1986; Wang *et al.*, 1995), China (Wang *et al.*, 1993a) and Scotland (Wilde *et al.*, 1986). Ir anomalies have been interpreted as evidence for meteorite

impacts, as Ir is usually of low abundance on the Earth's crust (Alvarez *et al.*, 1980). The minor Ir anomalies in the Upper Ordovician are not associated with other impact indicators (e.g. shocked quartz), and have been attributed to sedimentary condensation or increased erosion rather than a meteorite impact. Thus, the Ir excursion in the *persculptus* GBZ does not represent a correlatable geological event (Wilde *et al.*, 1986; Goodfellow *et al.*, 1992; Wang *et al.*, 1995).

Only a handful of geochemical studies have been conducted through Llandovery strata. They have involved studies of variations in $\delta^{13}C$, $\delta^{18}O$, and $^{87}Sr/^{86}Sr$. Through the Llandovery, the $\delta^{13}C$ value gradually increases and a positive $\delta^{13}C$ excursion occurs within the Aeronian (lower *sedgwickii* GBZ) in Scotland (Dob's Linn; Heath, unpublished Ph.D. thesis, Univ. Liverpool 1998), Estonia (Heath *et al.*, 1998) and Gotland (Wenzel & Joachimski, 1996; Wenzel, 1996). This $\delta^{13}C$ excursion can be correlated with a sea-level fall (the regressive phase of Global Cycle G2; Section 2.4), and has been attributed by some authors to cooling or renewed glacial conditions. However, the lack of a coincident positive $\delta^{18}O$ excursion, indicating cooling, makes this interpretation uncertain. A coincident positive excursion of $\delta^{18}O$ and $\delta^{13}C$ has been identified within the basal Wenlock (Sheinwoodian) in Estonia (Heath *et al.*, 1998; Figure 2.21) and Gotland (Wenzel & Joachimski, 1996; Wenzel, 1996), which has been attributed to cooling or glacial conditions.

Within the Llandovery, three high frequency $^{87}Sr/^{86}Sr$ cycles with an approximate duration of one conodont biozone have been identified by Ruppel *et al.* (1996; Figure 2.23). An increase in the $^{87}Sr/^{86}Sr$ ratio would be expected to accompany a sea-level fall, as a result of increased weathering. In fact, Ruppel *et al.* (1996) noted that the positive anomalies within the upper *staurognathoides* (regressive phase of cycle G3), mid- *celloni* (regressive phase of cycle G4) and lower *amorphognathoides* (regressive phase of cycle G5) CBZs correlated with sequence boundaries. Likewise, a decrease in the $^{87}Sr/^{86}Sr$ ratio would predictably accompany a sea-level rise, as a result of decreased weathering. Therefore, the bases of each of the global sea-level cycles (discussed in Section 2.4) should correlate with a decrease in the $^{87}Sr/^{86}Sr$ ratio. Falls in the $^{87}Sr/^{86}Sr$ ratio do occur around the bases of Global Cycle G4 (*celloni* CBZ) and G5 (*amorphognathoides* CBZ), but are not associated with the cycles earlier in the

Llandovery. The correlation may improve with increased frequency of sample points. At present, the $^{87}Sr/^{86}Sr$ curve only partially supports the global sea-level cycles discussed herein.

A gradual increase in $\delta^{34}S$ through the Llandovery was followed by a major fall in the Wenlock to Ludlow sediments of the Selwyn Basin (Goodfellow & Jonasson, 1984). This has been interpreted as indicating that the Selwyn Basin remained anoxic and isolated through the Llandovery (Goodfellow & Jonasson. 1984). The $\delta^{34}S$ data are not yet of high enough resolution to identify cycles within the Llandovery and so are not useful for correlation.

The geochemical data discussed above has been added to the biostratigraphical framework developed in Section 2.3, in order to develop an event framework for the Upper Ordovician and Lower Silurian (Figure 2.24). The end-Ordovician positive $\delta^{18}O$ and $\delta^{13}C$ excursion has proven a useful tool for correlation and a good climate indicator (e.g. Underwood *et al.*, 1997). The positive $\delta^{13}C$ excursion within the *sedgwickii* GBZ may in future be useful in correlation and in the determination of climate change. Future studies of geochemical 'events' within Ordovician and Silurian sediments may help to improve the resolution of correlation.

2.6 A Framework for the Upper Ordovician to Lower Silurian

The sea-level cycles can be added to the biostratigraphic event framework to create a standard framework for the Upper Ordovician to Lower Silurian (Figure 2.24). A summary of the correlation of the biostratigraphic, sea-level and geochemical data is presented below.

Global Cycle H1 is a minor transgressive-regressive cycle associated with the appearance of the *Hirnantia* Fauna, and is thought to occur within the *extraordinarius* GBZ. A positive $\delta^{13}C$ and $\delta^{18}O$ excursion indicates that this cycle occurs within the glacial maximum. This is followed by Global Cycle G1, which represents the major post-glacial transgression and extends from the *persculptus* GBZ to the *argenteus* GBZ and the entirety of the *kentuckyensis* CBZ. Global Cycle G1 can be divided into

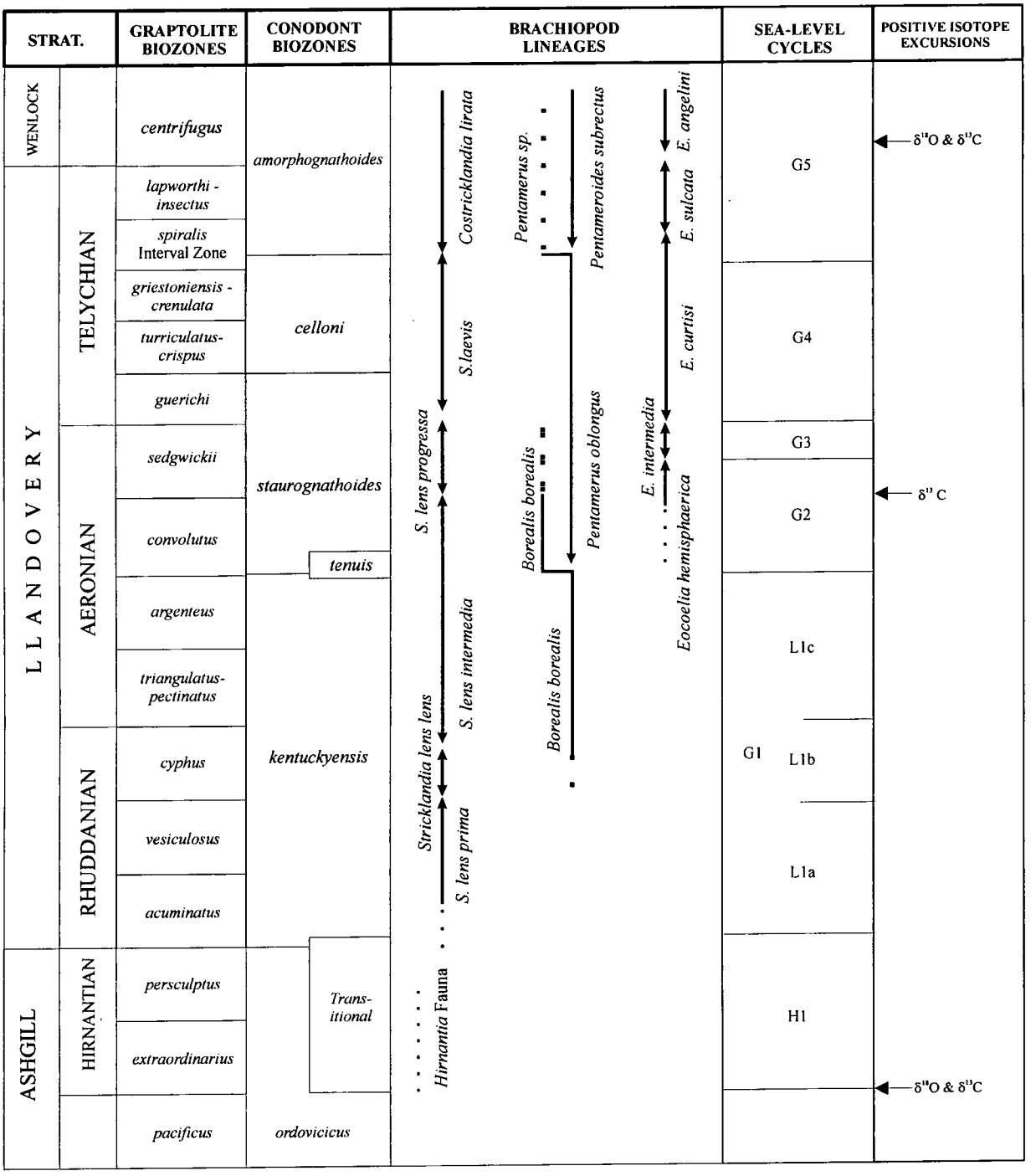


Figure 2.24 Upper Ordovician and Lower Silurian stratigraphical framework.

three cycles on Laurentia (L1a, L1b L1c). Laurentian Cycle L1a extends from the *persculptus* GBZ to the *vesiculosus* GBZ. It is associated with the basal part of the *kentuckyensis* CBZ. Laurentian Cycle L1b, which occurs within the *cyphus* GBZ, is associated with the appearance of the brachiopod genus *Virgiana* and / or *Borealis*. The youngest cycle (L1c) occurs between the *triangulatus-pectinatus* and *argenteus* GBZs, and the upper part of the *kentuckyensis* CBZ.

The transgressive base of Global Cycle G2 coincides with the first appearance of *Pranognathus tenuis* and / or *Distomodus staurognathoides*. It is associated with the *convolutus* GBZ and the first appearance of *Pentamerus* in shelf sections. The upper regressive part of Global Cycle G2 is associated with the extinction of *Pranognathus tenuis* and a positive $\delta^{13}C$ isotope excursion in the basal *sedgwickii* GBZ (Wenzel, 1996; Heath *pers. comm.*). Global Cycle G3 occurs within the upper *sedgwickii* GBZ and in shelf settings it is associated with the presence of the brachiopods *Pentamerus oblongus*, *Stricklandia lens progressa* and *Eocoelia intermedia*. It occurs within the upper part of the *staurognathoides* CBZ.

The transgressive base of Global Cycle G4a is coincident with the base of the *guerichi* GBZ and the appearance of *Eocoelia curtisi* and *Stricklandia laevis* in shelf sections. It may coincide with the first appearance of *Aulacognathus bullatus*, in sections were that species precedes the first appearance of *Pterospathodus celloni*. There is evidence that the base of Global Cycle G4b occurs within the *turriculatus-crispus* GBZ and is coincident with the first appearance of *Pterospathodus celloni* (*celloni* CBZ). The transgressive base of Global Cycle G5 occurs within the *spiralis* GBZ, and is associated with the first appearance of *Pterospathodus amorphognathoides*. *Pentameroides suberectus*, *Stricklandia lirata* and *Eocoelia sulcata* may also first appear at this point.

2.7 Relationship between stratigraphy and climate within the Upper Ordovician and Silurian

2.7.1 Glaciation during the Upper Ordovician and Lower Silurian

Evidence for glaciation in the Upper Ordovician has been well documented (for a review see Hambrey, 1985). It is generally thought that the initiation of the glaciation occurred in the early Ashgill and intensified, reaching a maximum, within the *pacificus* to *extraordinarius* GBZs. The end of the glacial maximum occurred prior to the *persculptus* GBZ (Brenchley *et al.*, 1995; Armstrong & Coe, 1997).

Evidence for renewed glacial conditions within the Silurian has been debated (e.g. Grahn & Caputo, 1992; Johnson, 1996). Silurian glacial deposits have been recorded in Peru, Argentina (Caputo & Crowell, 1985) and Brazil (Grahn & Caputo, 1992). Four discrete glacial horizons have been identified within the Parana Basin of Brazil, in the latest Ashgill / earliest Llandovery, early Aeronian, latest Aeronian / early Telychian, and late Telychian / early Wenlock (Grahn & Caputo, 1992). A lack of biostratigraphic data precludes well-constrained dating of the deposits, apart from the early Aeronian event, which has been dated within the *gregarius* GBZ (Grahn & Caputo, 1992). The *gregarius* GBZ correlates with the *triangulatus-pectinatus* to *argenteus* GBZs of the standard biozonal scheme (Rickards, 1995).

Comparison of relative global sea level with the occurrence of glacial deposits led Johnson (1996) to suggest that the four global sea-level cycles identified by him were consistent with the retreat and expansion of polar ice. However, as has been discussed above, a larger number of sea-level cycles can be identified within the Llandovery. The *gregarius* GBZ correlates with Global Cycle G1c, but it can not be determined whether the glacial deposits correlate with the transgressive or regressive phase of that cycle. The glacial deposits are so poorly constrained in age that it is difficult to determine whether they correlate with the global sea-level cycles.

The correlation of a positive $\delta^{13}C$ excursion (Wenzel, 1996; Heath, unpublished Ph.D. thesis, Univ. Liverpool, 1998) with a sea-level fall (Loydell, 1998) within the

sedgwickii GBZ, may indicate that cooling occurred within the Mid Aeronian. A positive $\delta^{13}C$ excursion does not in itself indicate cooling, as it merely represents changes in organic matter (Section 1.7.1). However, in the Hirnantian and Sheinwoodian positive $\delta^{13}C$ excursions can be correlated with positive $\delta^{18}O$ excursions, which can be used to indicate increased ice accumulation and cooling. Therefore, some authors have suggested that the positive $\delta^{13}C$ excursion within the *sedgwickii* GBZ may also be linked to a cooling episode (Heath, unpublished Ph.D. thesis, Univ. Liverpool, 1998).

A positive $\delta^{18}O$ and $\delta^{13}C$ excursion within the Sheinwoodian may correlate with the glacial deposits identified in the late Telychian to early Wenlock (Wenzel & Joachimski, 1996; Heath *et al.*, 1998). Improved dating of the glacial deposits is essential if a link between the isotope and sea-level data is to be made.

2.7.2 Comparison with Silurian oceanic episodes and events

Variations in lithology and conodont faunas within Silurian sediments led Jeppsson (1990) to develop an ocean-state model with two end members: Primo and Secundo Episodes (Figure 2.25). Primo Episodes (PE) were identified by argillaceous limestone deposition in shallow water and high-diversity conodont faunas, characterised by diverse and abundant panderodontids and the appearance of platform conodont taxa such as *Pranognathus*, *Pterospathodus*, *Apsidognathus* and *Aulacognathus* (Aldridge *et al.*, 1993b). They were interpreted as episodes of cooler high latitudes and humid low latitudes. Thermal contraction of the oceans and probable increase of ice-sheet formation resulted in falling sea level. The increased thermal gradient between high and low latitudes resulted in oceanic circulation, oxic deep waters and the deposition of limestones, grey-green shales and bioturbated sediments in deep water. In shallow water, an increase in argillaceous sediments and the lack of reef growth was attributed to increased continental weathering.

Secundo Episodes (SE) were identified by pure limestone deposition in shallow water and low-diversity conodont faunas dominated by species of *Ozarkodina* and coniforms (Aldridge *et al.*, 1993b). Drier low latitudes and warmer high latitudes

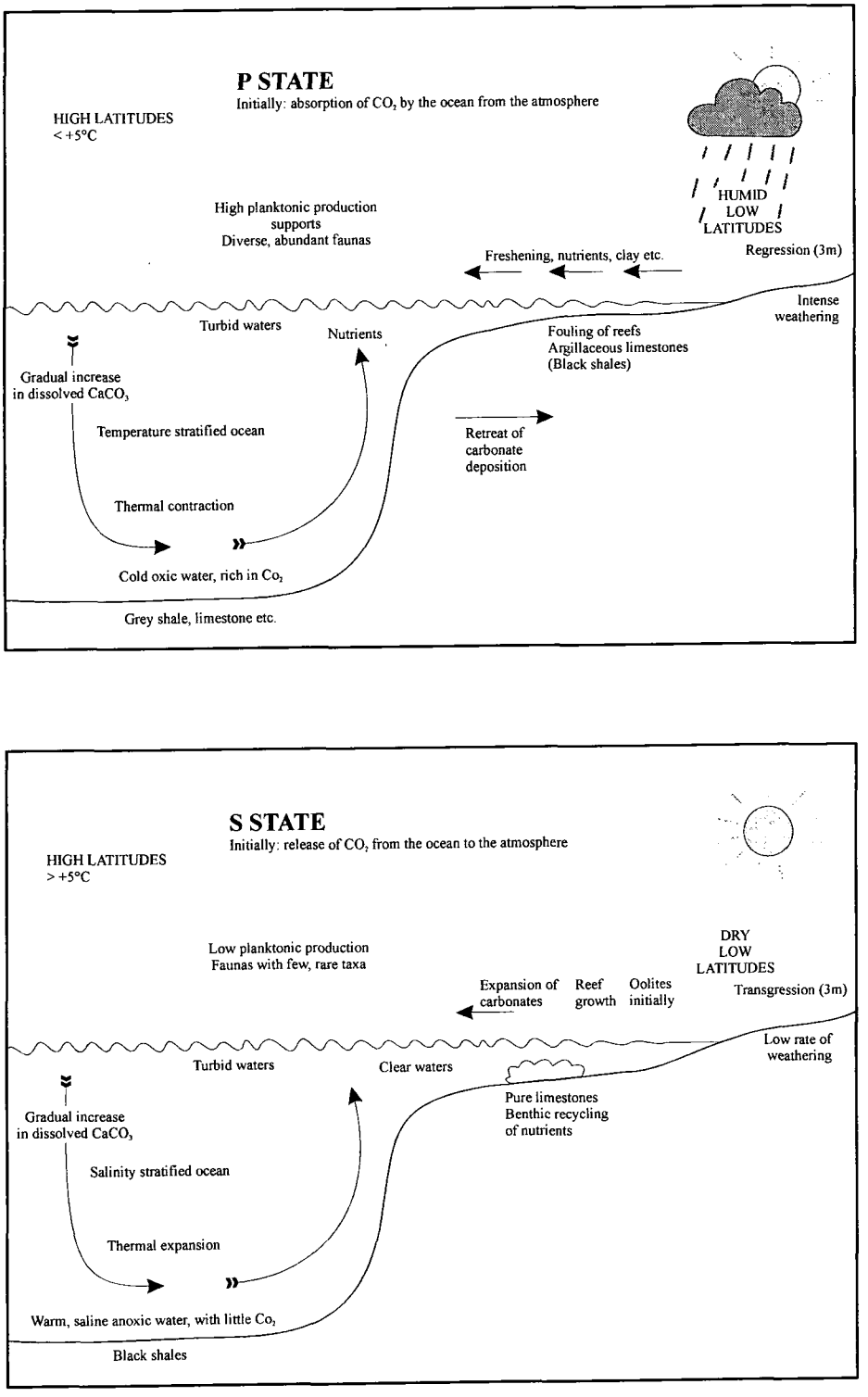


Figure 2.25 The characteristics of Primo (P) and Secundo (S) states. From Jeppsson (1990).

occurred during secundo episodes. The rate of continental weathering decreased and pure carbonates accumulated in shallow shelves. The increased temperature of the oceans and melting of ice sheets resulted in transgression. Cessation of ocean circulation resulted in anoxic deep waters and a decrease in available nutrients. The lack of nutrients and sediment-free shallow waters caused reefs to flourish.

Jeppsson (1990) suggested that 'Events' occurred during the transition from PE to SE, when fluctuating conditions caused stepwise extinction of conodont taxa. The transition from a SE to a PE was originally thought to be relatively smooth, but Jeppsson (1997) later suggested that events would also occur during the transition from SE to PE (Pri.-Sec. Event), following the identification of a graptolite extinction event by Loydell (1994), which correlated with a SE - PE transition.

Aldridge *et al.* (1993b) identified two oceanic cycles in the Llandovery to early Wenlock succession of Gotland and the Oslo Graben (Figure 2.26), which have not been fully documented in other areas. There have been mixed reports of supporting and contradictory data in the literature. Major reef-building events have been correlated with the S episodes by Brunton & Copper (1994) and Brunton *et al.* (1997), which is predicted by the model, but variations in graptolite diversity and deep-water facies do not support the model (Loydell, 1998).

Aldridge *et al.* (1993b) interpreted the uppermost Ordovician and basal Silurian as a secundo episode (Spirodden SE). The base of which was marked by the first appearance of *Ozarkodina hassi* and / or *Ozarkodina oldhamensis*. However, the first appearance of *Ozarkodina* occurs within Global Cycle H1, which has been correlated with the glacial maximum (Section 2.6). Jeppsson (1997) later reinterpreted the basal strata of the Spirodden SE as representing a Pri.- Sec. Event followed by a secundo episode within the Rhuddanian and lower Aeronian.

The subsequent cooling episode was termed the Jong PE (mid Aeronian); its base defined by the first appearance of the conodont *Pranognathus tenuis*, which can be correlated with the transgressive base of Global Cycle G2. The Jong PE and the subsequent Malmøykalven SE were separated by a period of climatic instability (Sandvika Event), which was not defined in terms of conodont appearances. The

extinction of *Pranognathus tenuis* and the deposition of less-argillaceous sediments were interpreted as marking the onset of the Malmøykalven SE (upper Aeronian). This period corresponds to the regressive phase of Global Cycle G2 and the entirety of Global Cycle G3. Jeppsson (1997) suggested the presence of a Sec.- Pri. Event between the Malmøykalven SE and the Snipklint PE, but this was not defined in terms of changes in the conodont fauna. The Snipklint PE (Lower Telychian) was characterised by the deposition of argillaceous sediments and spanned the *celloni* and *amorphognathoides* CBZs, which occur within Global Cycles G4 and G5, herein.

Comparison of the events and episodes with the sea-level cycles discussed above indicates that the base of the Jong PE and the Snipklint PE correlate with periods of transgression, rather than regression as is predicted by the Jeppsson (1990) model. The cooling episode within the basal *sedgwickii* GBZ identified by isotope data correlates with the Sandvika Event to Malmøykalven SE, which is a period of warming. The framework developed herein is not consistent with the episodes and events outlined by Aldridge *et al.* (1993b).

It should be noted that the lithologies within the Oslo – Asker District sections, where the Llandovery episodes and events were first identified by Aldridge *et al.* (1993b), also do not fit the ocean-state model of Jeppsson (1990). The Solvik Formation was defined as a secundo episode despite the dominance of siltstones and shales, and not pure carbonates, within that formation. The overlying Jong PE was identified in the upper Solvik Formation at a point where shale increased and siltstone and sandstone beds decreased (Aldridge *et al.*, 1993b). However, the Jeppsson (1990) model defined primo episodes as times of increased runoff and increased clastic input (i.e. siltstone and sandstone). Likewise, within the Snipklint PE Aldridge *et al.* (1993b) state that in some areas the basal Vik Formation is represented by dark, graptolitic shales. However, the appearance of graptolitic shales overlying limestone would be traditionally used to indicate deepening. The sea-level interpretation of the Oslo Graben section by Worsley (1989) and Johnson *et al.* (1991b) also suggests that some of the variations in lithology attributed to changes in ocean state could be alternatively interpreted as merely representing changes in sea level. Therefore, the evidence for the existence of oceanic episodes and events even in the Oslo – Asker District is not conclusive.

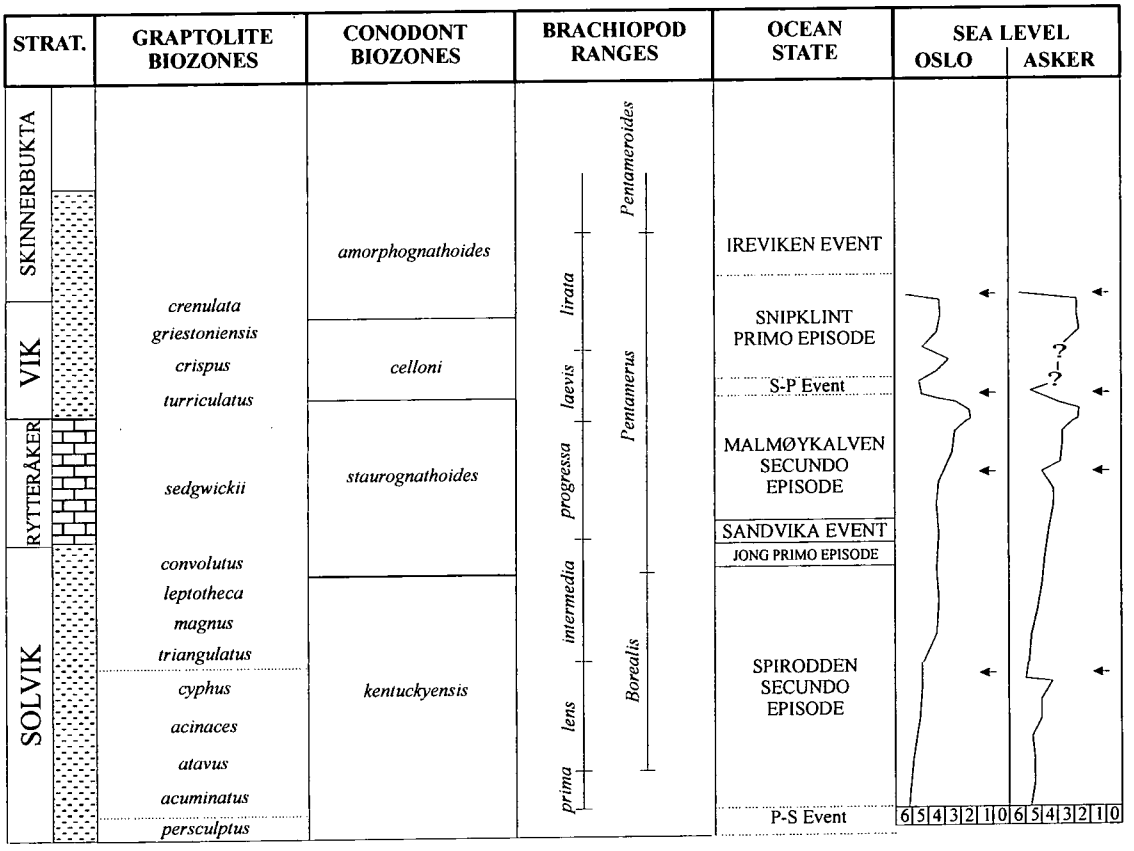


Figure 2.26 Correlation of the oceanic episodes and events proposed by Aldridge *et al.* (1993b) and Jeppsson (1997) in the Oslo Graben compared with biostratigraphical and sea-level data. Sea-level curve after Johnson *et al.* (1991). Lithological changes through the section have been discussed by Aldridge *et al.* (1993b) and Worsley (1989).

2.8 Conclusions

- The data available currently regarding the correlation of conodont, graptolite and brachiopod biozones has been reviewed and a biostratigraphical framework developed.

- Global and local sea-level cycles have been identified and compared using the biostratigraphic framework.

- Chemostratigraphical studies are at a preliminary stage and are in general not yet useful for correlation.

- A minor T-R cycle has been identified within the Hirnantian and at least five cycles can be identified within the Llandovery.

- Three cooling events may have occurred within the Upper Ordovician to Lower Silurian, within the Hirnantian, mid Aeronian and Sheinwoodian.

- The framework developed herein does not support the identification of oceanic episodes and events within the Llandovery, as outlined by Aldridge *et al.* (1993b).

Chapter 3

A Framework for Recovery: Correlation of Upper Ordovician and Lower Silurian Strata of Lake Timiskaming (Ontario), Anticosti Island (Québec) and Prongs Creek (northern Yukon).

Chapter 3

A Framework for Recovery: Correlation of Upper Ordovician and Lower Silurian Strata of Lake Timiskaming (Ontario), Anticosti Island (Québec) and Prongs Creek (northern Yukon).

3.1 Introduction

Within this thesis, conodont samples from three Upper Ordovician to Lower Silurian sections from different palaeogeographical settings have been studied; the inner-shelf section at Lake Timiskaming (Ontario), the mid-shelf Anticosti Island section (Québec), and the outer-shelf, Prongs Creek section (northern Yukon; Figure 3.1). All were situated on, or marginal to, the Laurentian craton, which was centered within the tropics during the late Ordovician and early Silurian.

The differences in depositional environments are reflected in the lithologies and faunas present. This chapter introduces the lithology, biostratigraphy, chemostratigraphy and sea-level cyclicity of the sections, and correlates them with the global standard framework discussed in Chapter 2.

The conodont samples from Lake Timiskaming and Prongs Creek were collected by A. D. McCracken and processed at the Geological Survey of Canada. The samples from Anticosti Island were collected and processed by the author.

3.2 Shallow water: Lake Timiskaming outlier, Ontario

Lake Timiskaming is situated on the border between Ontario and Québec (Figure 3.2). During the late Ordovician and early Silurian, a shallow seaway existed across this area, which is thought to have linked the Michigan and Hudson Bay Basins (Hume,

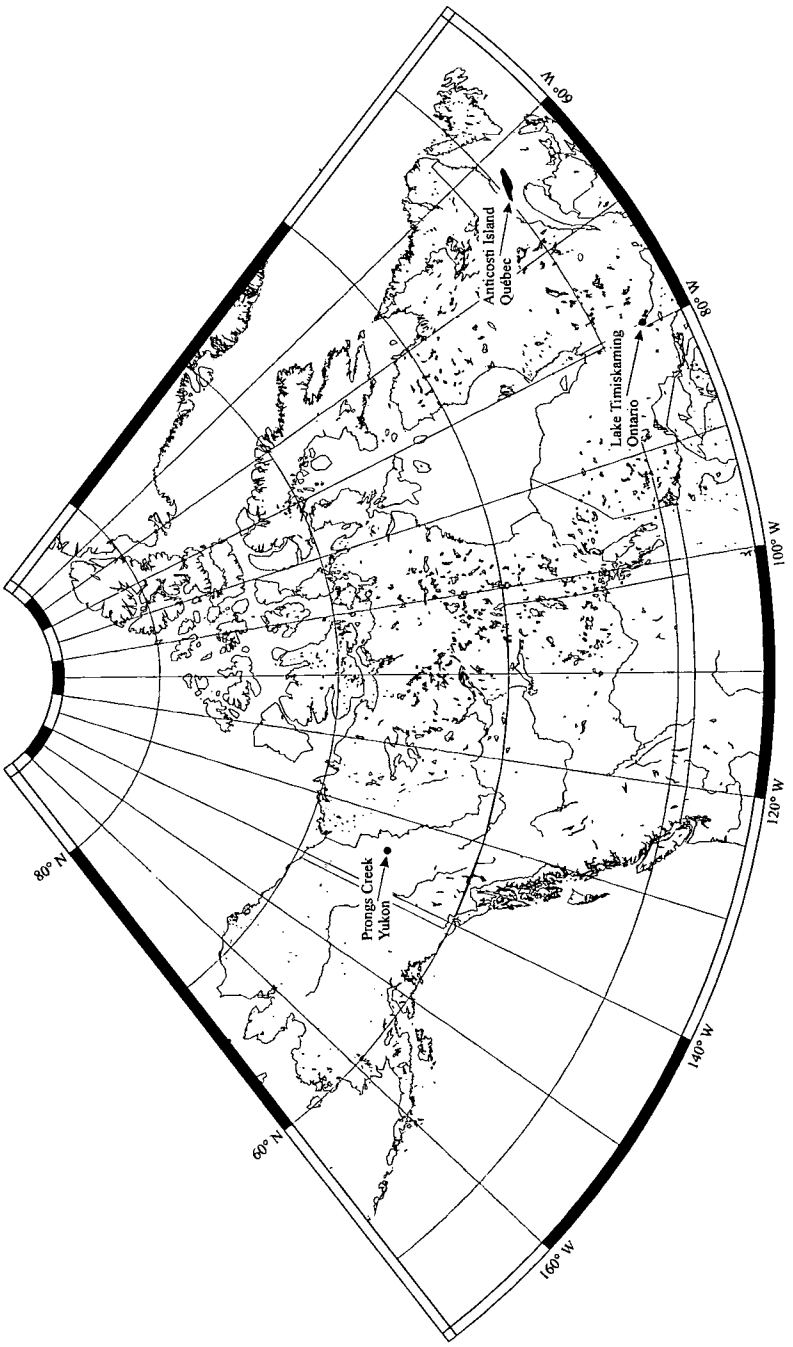


Figure 3.1 A map of Canada showing the locations of Lake Timiskaming, Anticosti Island and Prongs Creek.

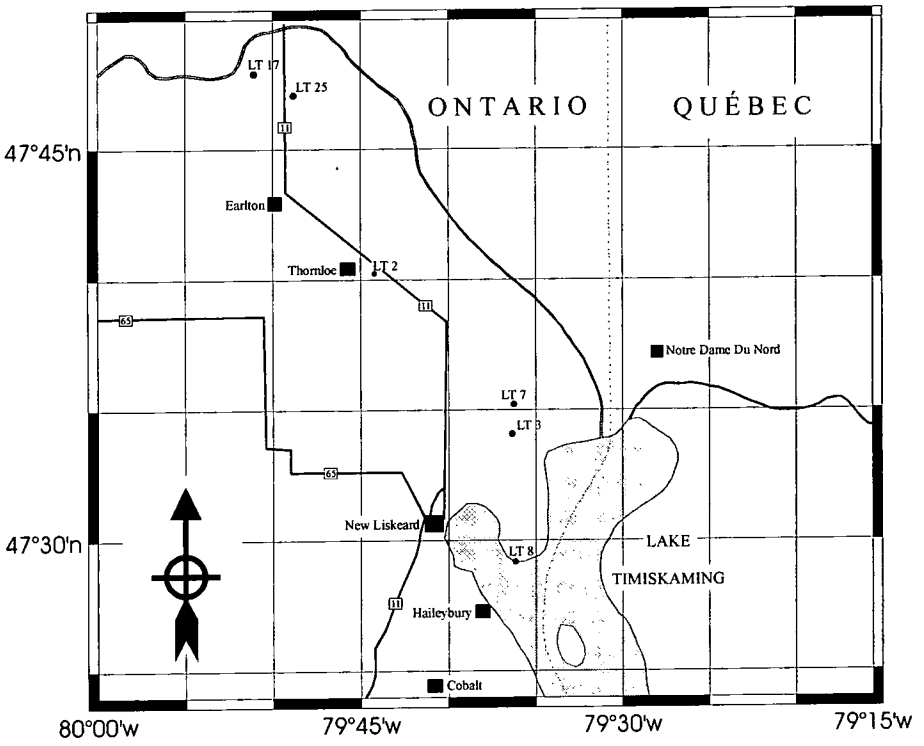


Figure 3.2 Conodont sampling localities in the Lake Timiskaming area: Loach Quarry (LT 2), Highway 65 Roadcut (LT 3), Middleton Quarry (LT 7), Dawson Point (LT 8), Evanturel Creek (LT 17) and McNamara Quarry (LT 25).

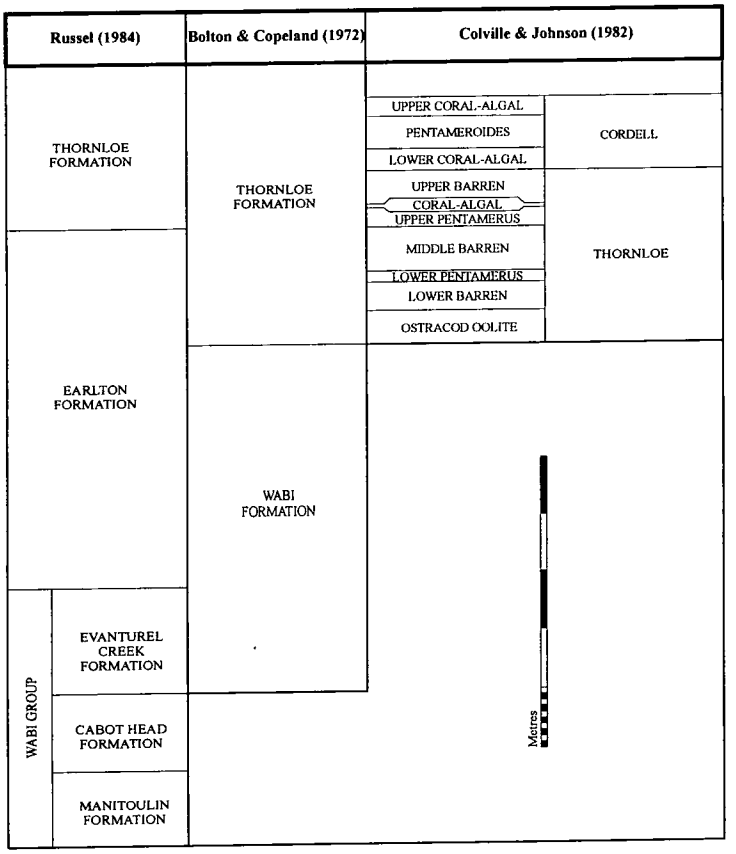


Figure 3.3 Correlation of stratigraphical schemes utilised for the Silurian strata of Lake Timiskaming.

1925). Upper Ordovician and Lower Silurian rocks crop out sporadically with the full succession only being known from a borehole (Thomson, 1965

The original stratigraphic framework was proposed by Hume (1925) and detailed maps of the area were first produced by Thomson (1956, 1965). The stratigraphic framework was revised following the drilling of the borehole, LT-1 (Thomson, 1965; Poole *et al.*, 1971). Ordovician strata (Liskeard Group) are subdivided into the Guiges (50.7m), Bucke (19.7m), Farr (4l.lm) and Dawson Point (27.9m) Formations (Russell, 1984). Russell (1984) divided the Silurian strata into the Manitoulin, Cabot Head, Evanturel Creek (17m), Earlton (62m) and Thornloe Formations (70m). The Manitoulin, Cabot Head and Evanturel Creek Formations have been united within the Wabi Group (Russell, 1984). The previous stratigraphic schemes for the succession are compared in Figure 3.3.

3.2.1 Lithology

The Ordovician rocks in the Lake Timiskaming area are variable and include siltstones, sandstones, shale, limestone and calcareous shales (Russell, 1984). Ordovician - Silurian boundary strata are not exposed. In the borehole LT-1, the basal bed of the Manitoulin Formation is a crinoidal grainstone, which 'sharply' overlies Ordovician shales (Russell, 1984). The Manitoulin Formation is predominantly composed of mottled dolostones with shale laminae, whilst the Cabot Head Formation is dominated by red shales which may be brecciated and interbedded with green shale, sandstone, or gypsum (Russell, 1984). The overlying Evanturel Creek Formation is predominantly composed of green, ripple-marked and mud-cracked mudstones and shales overlain by dolostones (Figure 3.4). Russell (1984) identified many additional lithologies in the Earlton Formation including intraformational conglomerates, oolitic and bioclastic limestones occurring in thin beds.

The Earlton Formation (62m) is characterised by limestones and dolostones with interbeds of bioclastic and oolitic limestone (Russell, 1984). The basal part of the formation is dominated by dolostone. Corals, gastropods and brachiopods (e.g. *Pentamerus*) are common. The base of the overlying Thornloe Formation (70m) is marked by a thick Pentamerid bed (upper *Pentamerus* Bed of Colville & Johnson,

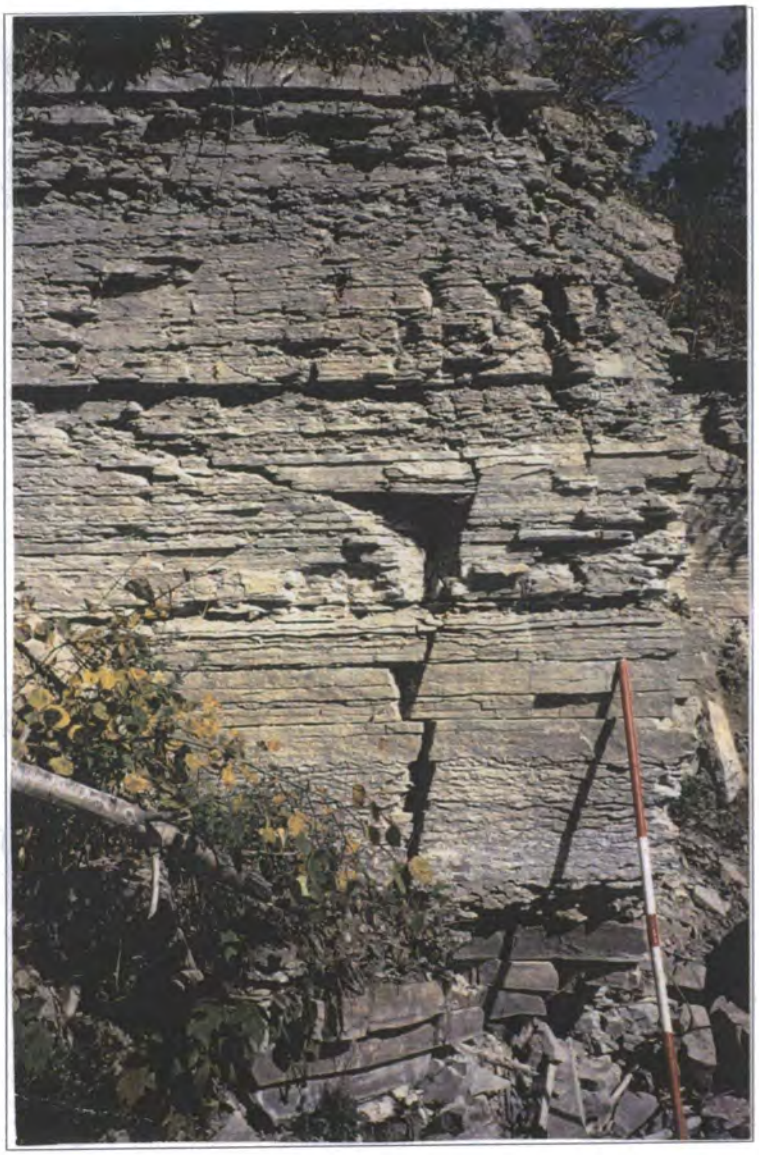


Figure 3.4 The Evanturel Creek Formation exposed at Evanturel Creek (Locality LT 17). Photograph taken by A. D. McCracken.

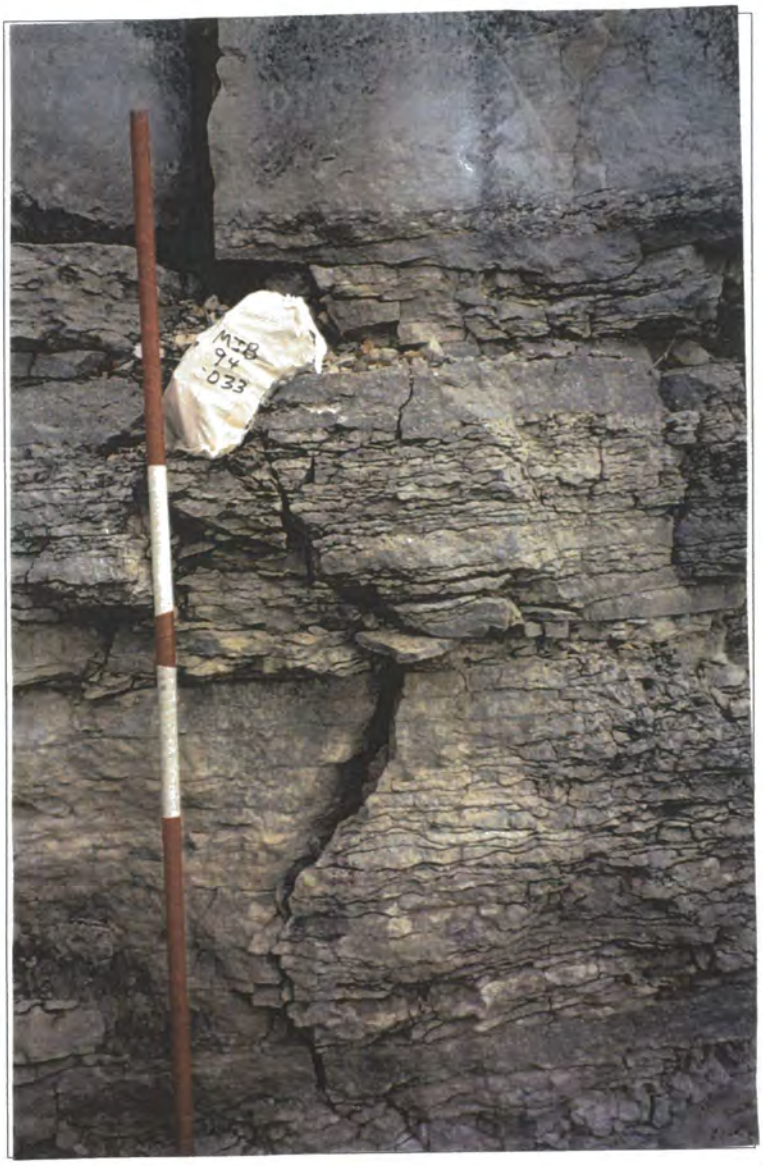


Figure 3.5 The Thornloe Formation at Dawson Point (Locality LT 8). Sample LT 272 was taken from the bed which the sample bag has been placed. The photograph was taken by A.D. McCracken.

1982) composed of fine-grained dolostone (Russell, 1984). In general, the lower part of the formation is characterised by dolostone with silicified corals, stromatolites and chert nodules, whereas the upper part consists of greenish-bluish dolostone (Russell, 1984; Figure 3.5).

A detailed study of the lithological changes through the upper Earlton and Thornloe Formations was conducted by Colville & Johnson (1982). They described lithological cycles consisting of *Pentamerus* or *Pentameroides*, Coral-algal, Ostracode-oolite, and Barren Beds. The *Pentamerus* Beds are characterised by fine-grained limestones with abundant tabulate and rugose corals in a mixed pentamerid-coral macrofauna. The *Pentameroides* Bed is composed of dolomite interbedded with white chert lenses, and yields *Pentameroides suberectus* with favositid and rugose corals, and stricklandiid brachiopods. The Coral-algal Beds are coarse-grained limestones, yielding *Favosites*, *Halysites*, *Syringopora*, *Arachnophyllum* and crinoidal debris. The Barren Beds are fine-grained, occasionally laminated, greenish limestone with mudcracks; they lack macro-fossils. The Ostracode-oolite Beds are characterised by oolitic limestones bearing ostracods, rhynchonellid brachiopods, high-spired gastropods and stromatoporoids (Colville & Johnson, 1982).

3.2.2 Biostratigraphy

3.2.2a Macrofauna

Bolton & Copeland (1972) described six faunal assemblages within the Silurian rocks of Lake Timiskaming (Figure 3.7). They recovered a specimen of the graptolite *Dictyonema* sp. from the Silurian succession, which is not age diagnostic. However, the pentamerids and other brachiopods within the Earlton and Thornloe Formations are useful for age determination. The Upper *Pentamerus* Bed (basal Thornloe Formation) yields rare specimens of *Eocoelia curtisi*, which indicates an early Telychian age (Colville & Johnson, 1982). The *Pentameroides* Bed (mid Thornloe Formation) yields *Pentameroides suberectus*, *Costistricklandia multilirata* and the rugose coral *Porpites*, which suggest a late Telychian or early Sheinwoodian age (Colville & Johnson, 1982).

Herein, thelodonts have been recovered from the Evanturel Creek Formation (samples LT 261 and LT 269) indicating a broad Lower Silurian age (I. J. Sansom *pers. comm.*).

3.2.2b Microfauna

Previous conodont studies of the rocks around Lake Timiskaming have been limited to an unpublished study through the Ordovician strata (Munro, Unpublished MSc. Thesis, 1975) and the description of two conodont specimens from the Silurian strata by Bolton & Copeland (1972). An element described as '*Icriodella* sp.' was recorded from the Evanturel Creek Formation and a specimen of '*Ligonodina*? sp.' from the Thornloe Formation (Bolton & Copeland, 1972).

The samples studied herein were collected through the Silurian strata at seven localities (Figure 3.2). A total of seventeen samples have been studied from the Evanturel Creek Formation (Loach Quarry, LT 2; Evanturel Creek, LT 17), the mid Earlton Formation (Highway 65 Roadcut, LT 3), and the basal Thornloe Formation (Mcnamara Quarry, LT 25; Dawson Point, LT 8; Middleton Quarry, LT 7; Figure 3.2). The conodont species recovered from the samples are shown in Figure 3.6.

The samples from Evanturel Creek were dominated by *Icriodella deflecta* (up to 33%) and *Icriodella discreta* (up to 54%). *Kockelella manitoulinensis* occurs in one sample (LT 262), where it constitutes 18% of the fauna. Other taxa that are not found in all samples through the Evanturel Creek Formation include *Ozarkodina oldhamensis*, *Ozarkodina hassi*, *Oulodus petilus*, *Panderodus acostatus*, *Panderodus* sp. A, and *Decoriconus fragilis* (Figure 3.6). The fauna is indicative of the *kentuckyensis* CBZ, but *Distomodus kentuckyensis* has not been recovered. A species of *Distomodus* (*Distomodus* ? sp. A), which lacks the distinctive four-processed P element of *Distomodus kentuckyensis*, is present in one sample (LT 267).

The few samples collected from the Earlton Formation, yielded a fauna dominated by *Oulodus petilus* (up to 42%), *Kockelella* sp. B (up to 40%), *Ozarkodina* cf. O. sp. C Armstrong (up to 41%), and *Panderodus unicostatus* (up to 29%). A new species of

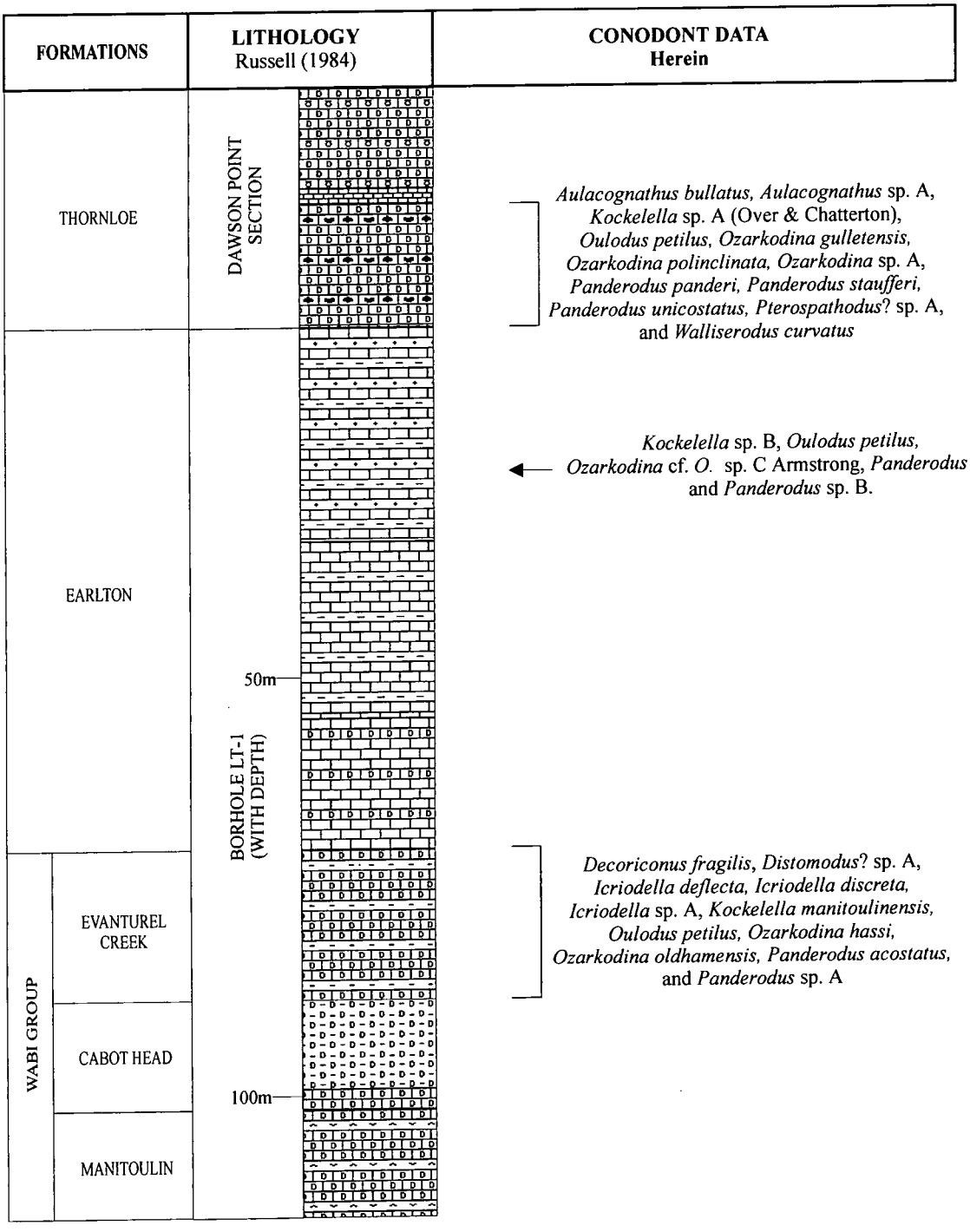


Figure 3.6 Conodont faunas recovered from the Lake Timiskaming section compared to the general stratigraphical log of Russell (1984). Refer to Figure 3.7 for the lithological key.

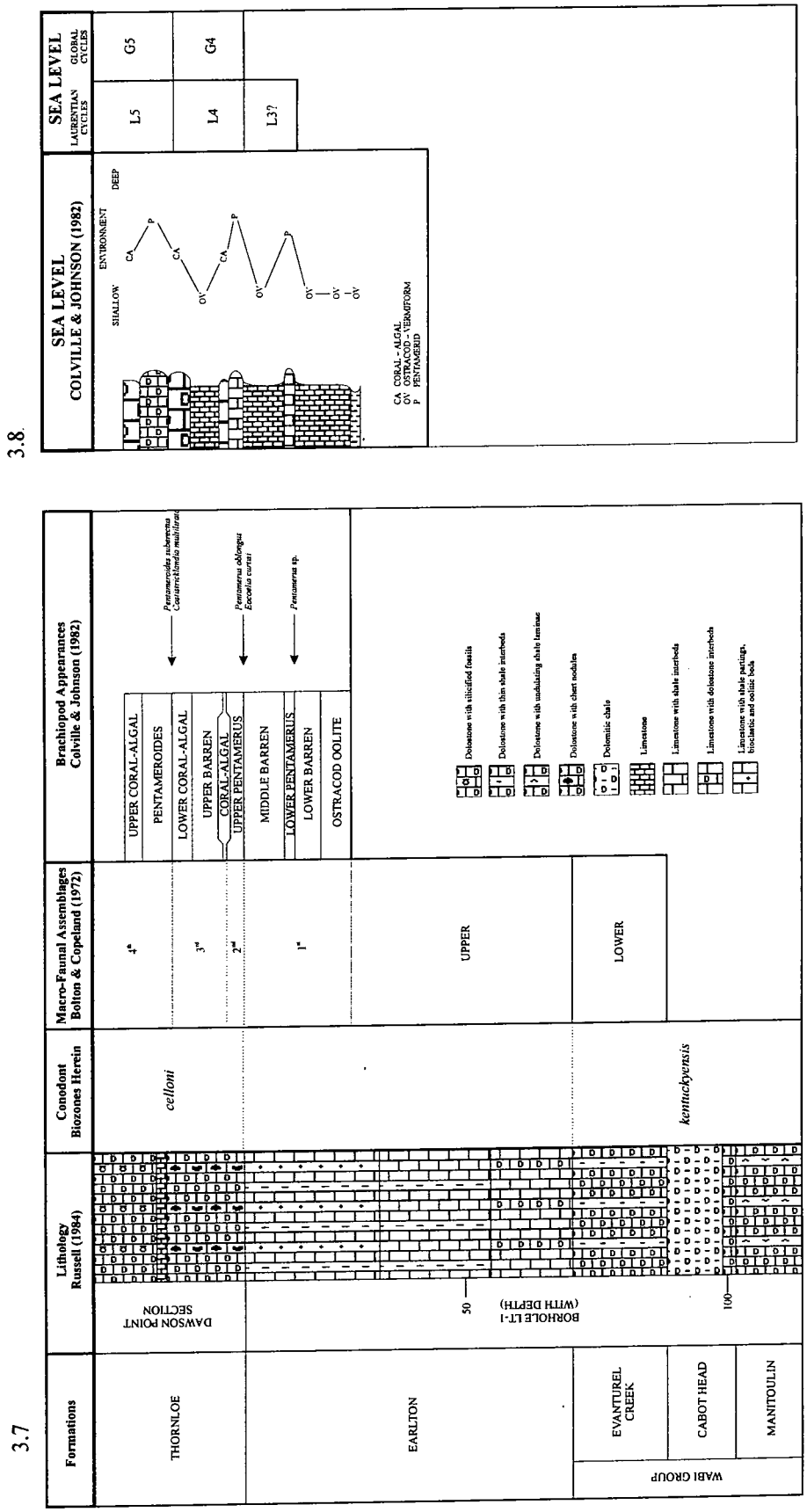
Panderodus, *Panderodus* sp. B, occurs in sample LT 265. The lack of diagnostic taxa inhibits the correlation of this formation with the standard conodont biozonal scheme.

Samples from the base of the Thornloe Formation (LT 253, LT 270) yielded *Aulacognathus bullatus* (up to 17%), *Ozarkodina gulletensis* (up to 44%), *Ozarkodina polinclinata* (up to 15%), *Oulodus petilus* (up to 24%), *Panderodus panderi* (6%), and *Panderodus unicostatus* (5%). The taxa are indicative of strata within or just below the *celloni* CBZ. Although, elements of *Pterospathodus celloni* are absent, the presence of a new species of *Pterospathodus*, *Pterospathodus* n. sp. A (up to 23%), allows tentative correlation with the *celloni* CBZ. Taxa that appeared in younger samples within the Thornloe Formation include *Aulacognathus* sp. A, *Panderodus staufferi*, *Walliserodus curvatus*, and *Ozarkodina* sp. A. Additionally, *Kockelella* sp. A (Over & Chatterton) was recovered from samples LT 279 and LT 278.

3.2.3 Chemostratigraphy and sea-level cyclicity

There have been no geochemical studies of the section at Lake Timiskaming. However, a study of the sea-level fluctuations was conducted by Colville & Johnson (1982). They constructed a sea-level curve, from interpretation of the changing faunal assemblages within the upper Earlton and Thornloe Formations (Figure 3.8). They identified peak transgressions marked by abundant pentamerids (*Pentamerus* or *Pentameroides* Beds) and peak regressions marked by the ostracod vermiform or Barren Beds. The Coral-algal Beds were interpreted as representing intervening transgressive-regressive phases.

Three peak transgressions were identified within the Lower *Pentamerus* Bed (upper Earlton Formation), Upper *Pentamerus* Bed (basal Thornloe Formation), and *Pentameroides* Bed (upper Thornloe Formation; Colville & Johnson, 1982). The lack of diagnostic fossils inhibits the comparison of the Lower *Pentamerus* Bed transgression with the global sea-level cycles discussed in Chapter 2. However, the occurrence of *Eocoelia curtisi* and conodonts indicative of the *celloni* CBZ within the Upper *Pentamerus* Bed suggests correlation with Global Cycle G4. Likewise, the



Figures 3.7 and 3.8 Summary of currently available biostratigraphical data for the Lake Timiskaming section. The sea-level curve of Colville & Johnson (1982) for the Earlton and Thornloe Formations compared with global sea-level cycles.

presence of *Costistricklandia multilirata* within the *Pentameroides* Bed suggests correlation with the Global Cycle G5.

3.3 Mid-Outer shelf: Anticosti Island, Québec

Anticosti Island is situated in the Gulf of St. Lawrence within the Province of Québec (Figure 3.9). During the Ordovician and Silurian, the Anticosti Basin was part of a tropical carbonate ramp close to the continental margin of Laurentia. Deposition was rapid (Copper & Jin, 1995) and the ramp deepened into the Iapetus Ocean to the southeast and shallowed towards a landmass in the northwest (Sami & Deroches, 1992)

Richardson (1857) first studied the stratigraphy and palaeontology of Anticosti Island and Schuchert & Twenhofel (1910) proposed a formal stratigraphy. Stratigraphical revisions were undertaken by Bolton (1972) and Petryk (1981a). The Ordovician strata are sub-divided into the Macasty, Vauréal and Ellis Bay Formations (Petryk, 1981a). The Macasty and lower Vauréal Formations are not exposed. The Vauréal Formation is overlain by the 'Gamachian' (Richmondian) Ellis Bay Formation.

Lower Silurian strata are sub-divided into the Becscie, Gun River, Jupiter and Chicotte Formations (Schuchert & Twenhofel, 1910). An additional Merrimack Formation was erected by Copper & Long (1989), for strata previously included in the Becscie Formation. Members within the Ellis Bay and Jupiter Formations were revised by Long & Copper (1987) and Copper & Long (1990), respectively. Members within the Vauréal and Chicotte Formations are currently informal (see Long & Copper, 1994). The current stratigraphic scheme is depicted in Figure 3.10.

3.3.1 Lithology

The exposed Vauréal Formation consists of interbedded calcareous and terreginous mudstones, and packstones, deposited in a mid- to outer-shelf setting (Long & Copper, 1994). The overlying Ellis Bay Formation varies across the island. Outcrops in the east (52m) consist of mixed carbonates and sandstones, whereas in the west

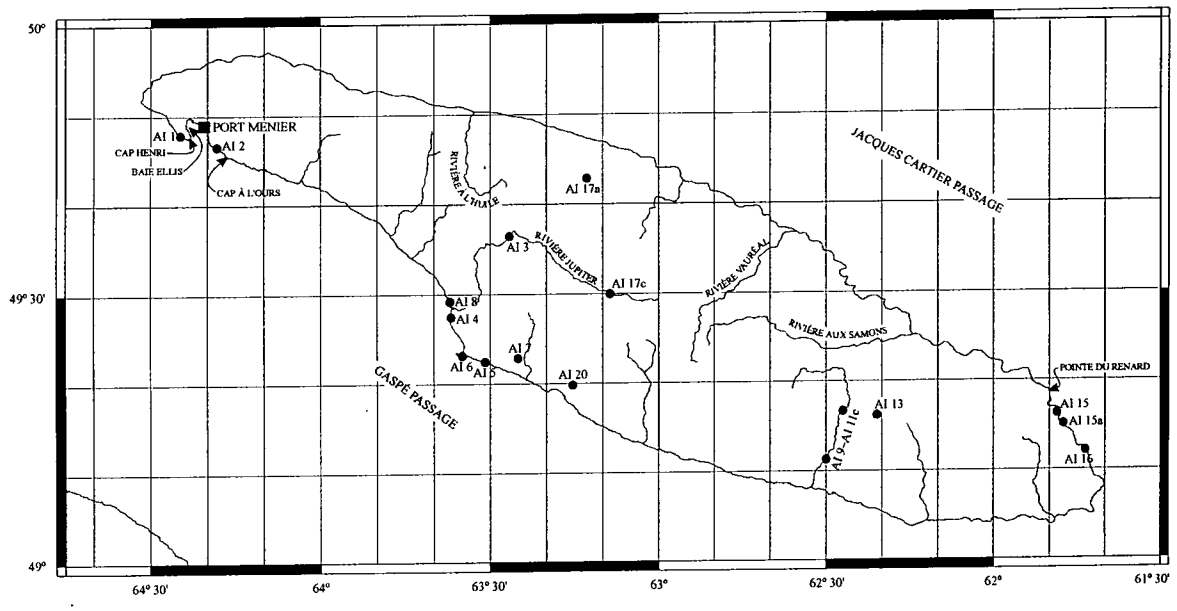


Figure 3.9 Conodont sampling localities on Anticosti Island: Point Laframboise (AI 1), Cap à 1' Aigle (AI 2), Jupiter 24 Lodge (AI 3), Cap Ottawa (AI 4), Brisants Jumpers (AI 5), Pointe du sud-ouest (AI 6), Rivière du Brick Road (AI 7), Cap Jupiter (AI 8), Rivière Dauphine Road (AI 9, AI 10b, AI 11b, AI 11c), Main Sandtop Road (AI 13), Baie Innommée (AI 15), Meeting of Sandtop road and Ruis de la Chute (AI 15a), Cap Sandtop (AI 16), Lac Wickenden Road (AI 17a, AI 17c), and Rivière Galiote Road (AI 20).

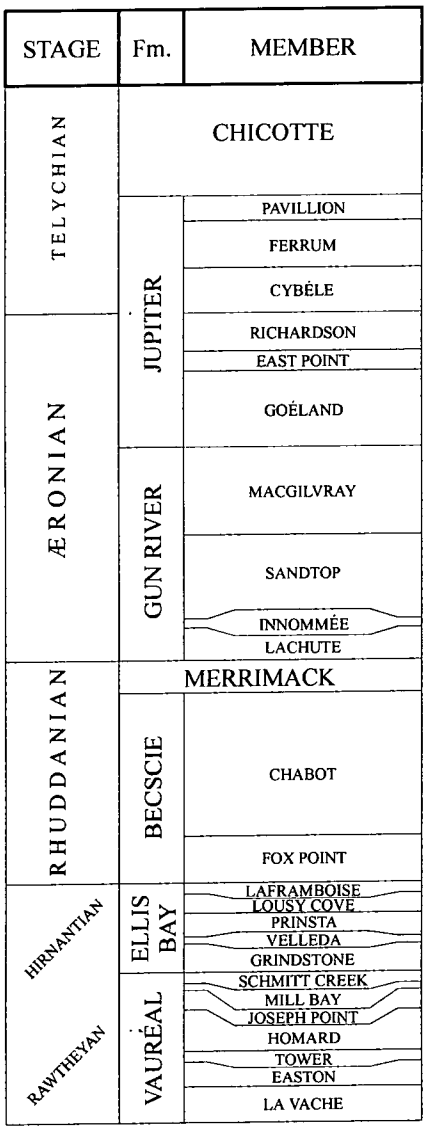
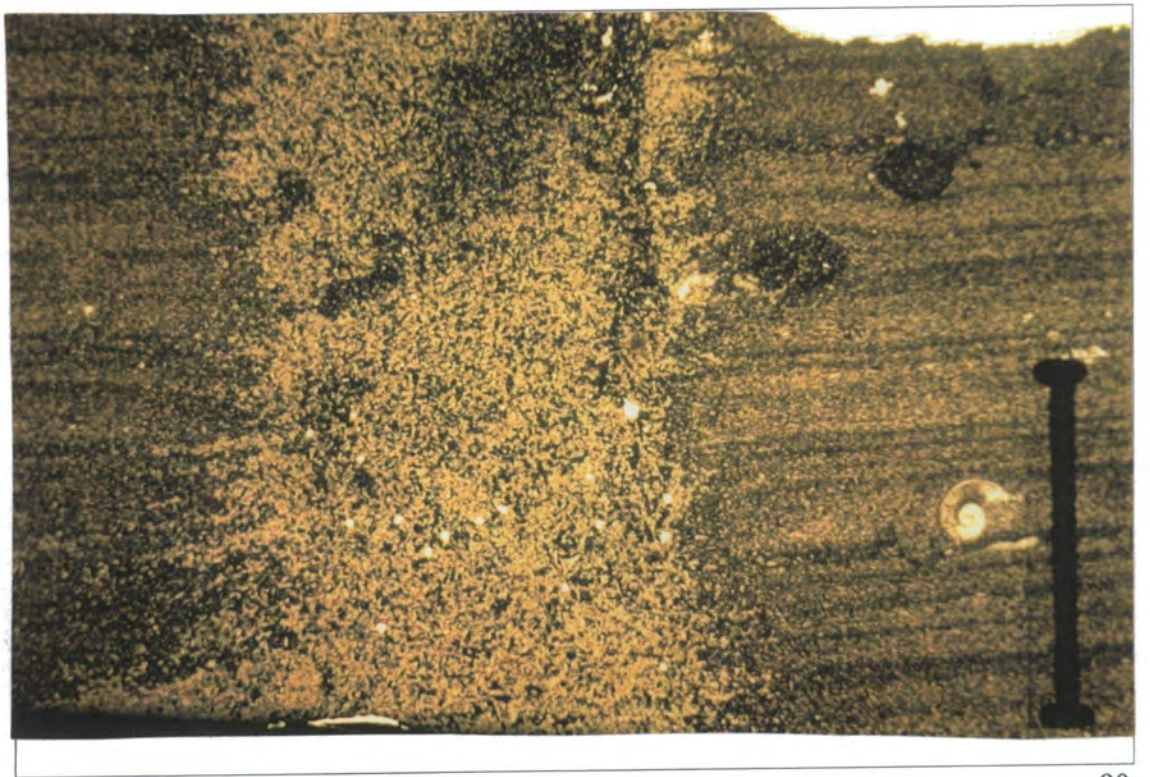


Figure 3.10 The stratigraphy of the Anticosti Island section.

Figure 3.11 Lousy Cove Member, the uppermost bed. Taken at Point Laframboise (Locality AI 1).

Figure 3.12 An acetate peel of the uppermost bed of the Lousy Cove Member (Sample AI 603 from Cap à 1' Aigle; Locality AI 2). Scale bar equals 1cm.



(72m), calcareous and terreginous mudstones predominate (Long & Copper, 1994). The formation can be divided into the Grindstone, Prinsta, Velleda, Lousy Cove and Laframboise Members, which can be traced across the island (Long & Copper, 1987).

The Lousy Cove and Laframboise Members and the basal beds of the overlying Becscie Formation have been extensively studied, following the nomination of the section on the west side of Ellis Bay as a possible international boundary stratotype for the base of the Silurian (Lespérance, 1981). The Lousy Cove and Laframboise Members are of interest herein, as it is within these strata that the end-Ordovician mass extinction event occurred.

The Lousy Cove Member comprises 16m of nodular calcareous mudstones, interbedded terreginous and calcareous mudstones and rare sandstones (Long & Copper, 1987). Fossils are intermittently abundant and include brachiopods (*Hindella*, *Dalmenella*, *Fardenia*, *Eostropheodonta* and *Hirnantia*), crinoid ossicles, with rare nautiloids, stromatoporoids (e.g. *Aulacera*) and corals (Long & Copper, 1987). The uppermost bed of the Lousy Cove Member bears hummocky cross stratification (Long, 1993; Figure 3.11). The bed is composed of a cream-coloured, calcareous mudstone containing 5 to 10% quartz grains. The bulk of the bed is composed of laminated micrite, with ferroan calcite concentrated in the bioturbated sections (Figure 3.12). The replacement of Ca^{2+} by Fe^{2+} is regarded as occurring under reducing conditions created by the decay of organic matter during diagenesis (Tucker, 1991). The bed contains a sparse fauna of gastropods, crinoid ossicles and brachiopods.

The Laframboise Member includes the Oncolite Platform Bed (O.P.B.) overlain by a Bioherm Unit. The O.P.B. is a highly resistant, limestone marker bed, which has a wackestone – grainstone texture and extends across the whole island. It is a very distinctive bed containing oncoids (Type C and Type R; Logan *et al.*, 1964) and bioclasts including crinoids, brachiopods, gastropods and corals in a sparry cement (Figure 3.13). The base of the O.P.B. contains rip-up clasts of the underlying bed (Orth *et al.*, 1986) and intraformational conglomerates (Cocks & Copper, 1981) indicating scouring and erosion. However, there is no reported evidence of sub-aerial exposure (Orth *et al.*, 1986). It contains Type C oncoids, which indicate that algal growth was interrupted with periods of slow sedimentation. Slow sedimentation is

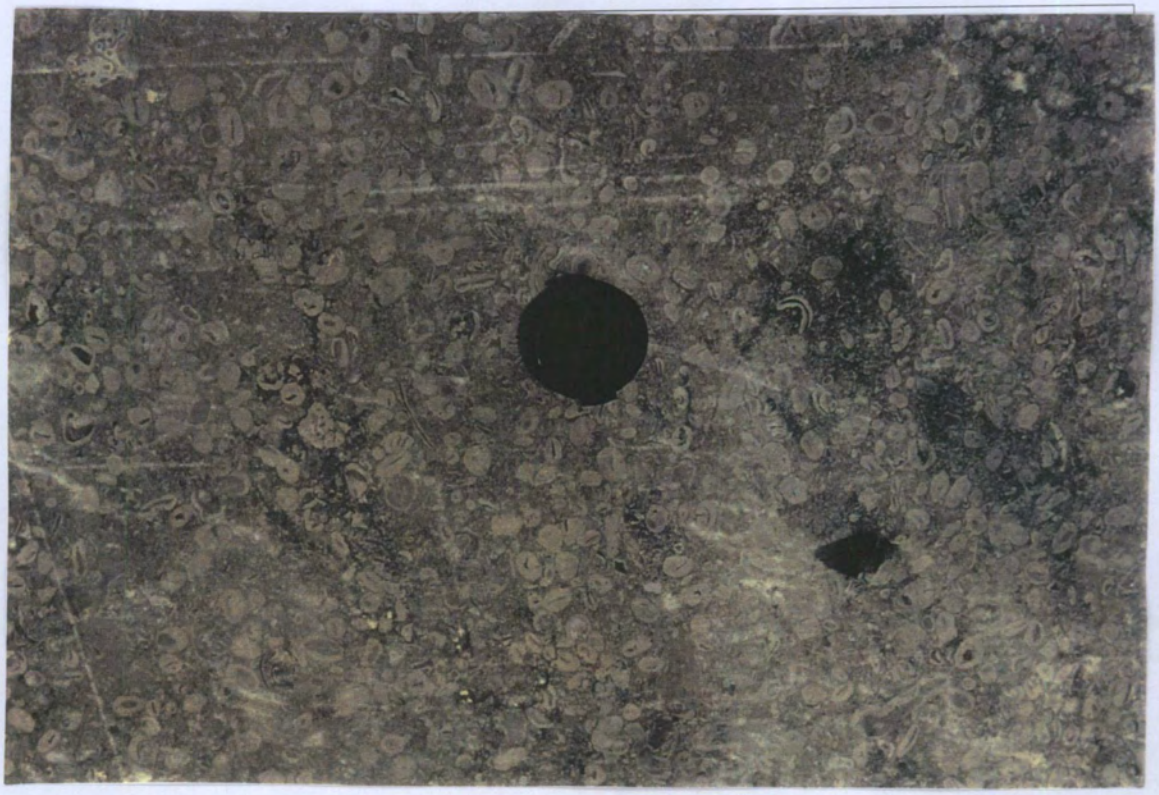


Figure 3.13 A bedding plane within the Oncolite Platform bed, exposed in a road cutting along Sandtop Road.

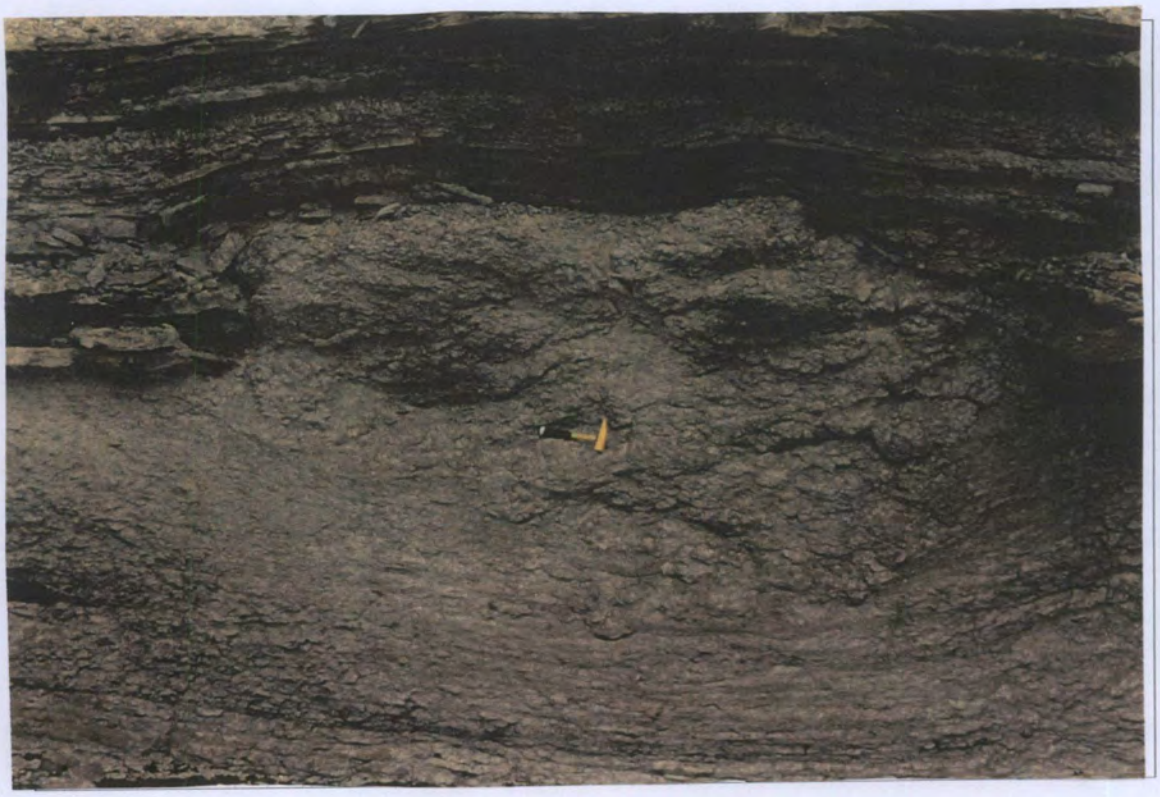


Figure 3.14 Bioherm Unit of the Laframboise Member at Point Laframboise (Locality AI 1).

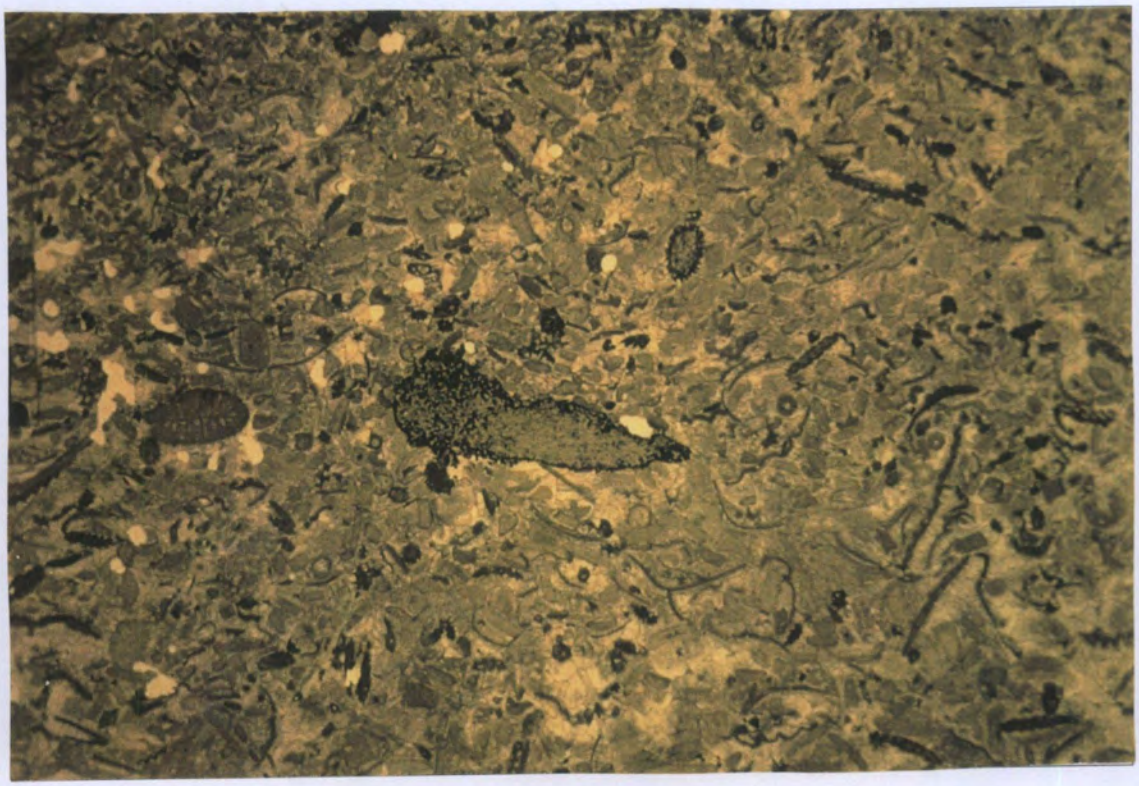


Figure 3.15 An acetate peel of the crinoid blanket (basal Becscie Formation), sample AI 577, Cap à 1' Aigle (Locality AI 2). Scale bar equals 1cm.

also indicated by multiple hard or firm ground surfaces at the base of, within and at the top of, the O.P.B. (Lake, 1981).

The Bioherm Unit contains small bioherms, interbedded with fine-grained limestones. The bioherms are rich in calcareous algae, tabulate corals, rugosans, stromatoporoids, and bryozoa (Long, 1993; Figure 3.14). The inter-bioherm sediments are highly bioturbated, nodular floatstones with local grainstones, intraformational conglomerates and oncolitic grainstones (Long & Copper, 1994). The beds are sparsely fossiliferous, but do yield crinoidal debris, broken gastropods, brachiopods and trilobites (Long & Copper, 1994).

The base of the Becscie Formation is a crinoidal grainstone (crinoid blanket) overlain by a thick sequence of fine-grained limestones and tempestites (Sami & Deroches, 1992). The crinoid blanket is composed of bedded grainstones and packstones (Lake, 1981). Bioclasts include crinoids, brachiopods, corals, bryozoa and rare trilobites. Acetate peels have shown syntaxial cements and diagenetic pyrite clasts can be seen under the microscope (Figure 3.15). The source of the crinoid grains may be a crinoidal bank or shoal adjacent to the bioherms (Lake, 1981; Sami & Deroches, 1992).

The Becscie Formation can be sub-divided into the basal Fox Point Member and the overlying Chabot Member (see Long & Copper, 1994). The Chabot Member is characterised by abundant storm-generated grainstones and intraformational conglomerates (Long & Copper, 1994). The fauna includes abundant tabulate and rugose corals, and brachiopods including dalmanellids and the pentamerid *Virgiana* (Long & Copper, 1994).

The Merrimack Formation (25m) is composed of recessive, calcareous shales and interbedded tempestites with an abundant brachiopod fauna (Copper & Long, 1989; Figure 3.16). The overlying Gun River Formation (133m) is predominantly characterised by rhythmically interbedded calcareous and terreginous mudstones (Long & Copper, 1994; Figure 3.17). It has been divided informally into the Lachute, Innommée, Sandtop and Macgilvray Members (Long & Copper, 1994).

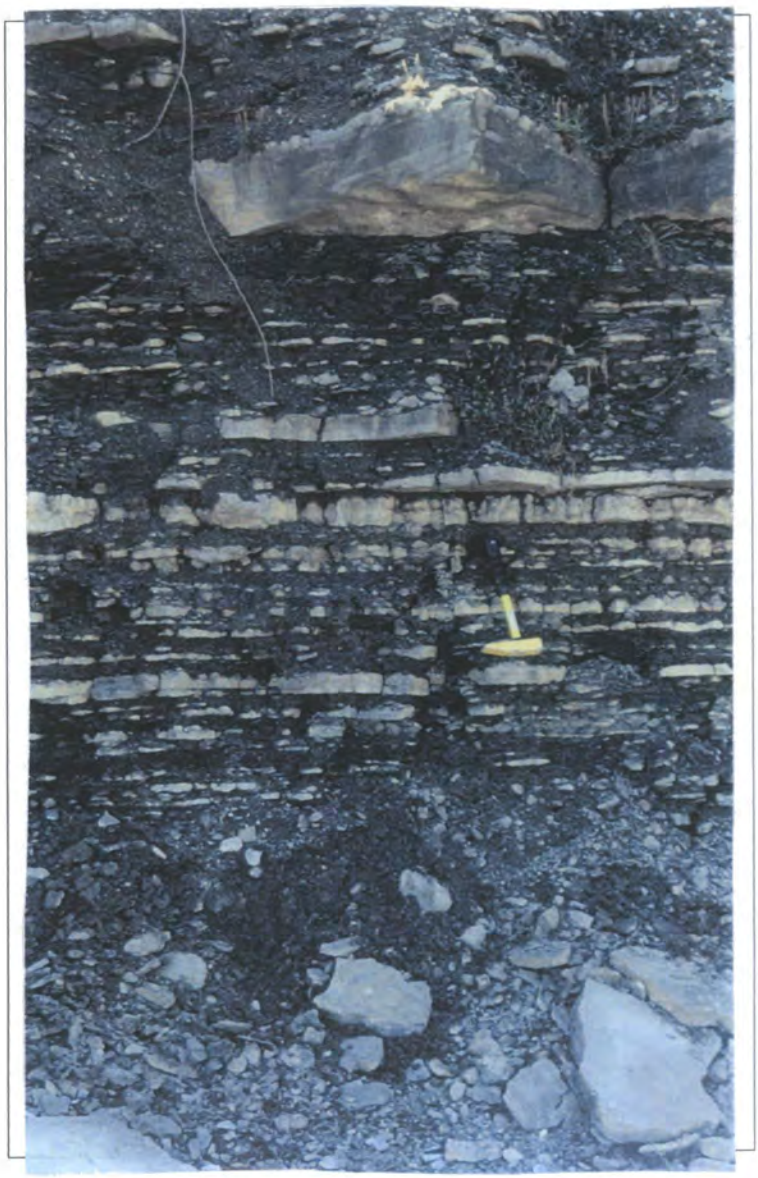


Figure 3.16 The basal part of the Merrimack Formation at Bay Innommée (Locality AI 15)

Figure 3.17 The Sandtop and Macgilvray Members of the Gun River Formation at Sandtop Cliffs (Locality AI 16).

Figure 3.18 The boundary between the Richardson and Cybéle Members of the Jupiter Formation at Cap Jupiter (Locality AI 8).

The Jupiter Formation comprises the Goéland, East Point, Richardson, Cybéle, Ferrum and Pavillion Members (Long & Copper, 1994). The Goéland Member (55m) is composed of interbedded wackestones and argillaceous mudstones, which are commonly calcareous (Copper & Long, 1990). It is very fossiliferous and yields abundant brachiopods, including pentamerids. It is overlain by the East Point Member (~10m) composed of red crinoidal grainstones with bioherm development in the eastern part of the island (Copper & Long, 1990). The succeeding argillaceous limestones of the Richardson Member (16m) bear a low diversity macro-fauna, which includes brachiopods (rhynchonellids, *Eocoelia* and *Clorinda*), graptolites and favositids (Copper & Long, 1990; Figure 3.18). The Cybéle Member (38m) is dominated by storm-generated wackestones, which are bioturbated with hardgrounds occurring sporadically (Copper & Long, 1990). The member is largely unfossiliferous, but rare graptolites and large trilobites occur. The Ferrum Member (~32m) is characterised by a marked lithological variability, with thinly bedded wackestone – packstones, calcareous shaley partings, hardgrounds and intraformational conglomerates (Long & Copper, 1994). The fauna includes many brachiopods and corals. The Pavillion Member (~12m) comprises calcareous, argillaceous shales, interbedded mudstone - wackestones with lenses of bioclastic packstones (Long & Copper, 1994). This member is rich in brachiopods and also bears corals and stromatoporoids.

The youngest Chicotte Formation (~90m) is composed of massive crinoidal-grainstone with patch reefs developed at at least three horizons. The reefs are up to 100m in diameter (Brunton & Copper, 1994). Brachiopods are rare. Emergence and associated karst development periodically occurs (Brunton & Copper, 1994). This formation has been informally divided into the Brisantes, Galiote and Babineau Members (Long & Copper, 1994).

3.3.2 Biostratigraphy

3.3.2a Macrofauna

Graptolites are rare in the Anticosti Island succession, but a number of age-diagnostic taxa have been recovered. The *complanatus* GBZ occurs within the basal Vauréal Formation, which is not exposed at the surface (Riva, 1988; Stewart & Mitchell, 1997; Figure 3.19). The *promiens* GBZ occurs through the Lavache to Tower Members of the Formation (Riva, 1988; Stewart & Mitchell, 1997). Graptolites of the *sedgwickii* GBZ are found in the Richardson and Cybéle Members of the Jupiter Formation (Riva & Petryk, 1981). *A. atavus* was recovered from the Sandtop Member of the Gun River Formation, indicating an age range from the *vesiculosus* to *gregarius* GBZs or *atavus* to *angulatus* GBZs (Riva & Petryk, 1981). *Normalograptus scalaris ferganensis* ranges from the upper *acinaces* GBZ to *convolutus* GBZ, and occurs within the basal member of the Jupiter Formation (Loydell, *pers. comm.*). Within this study, isolated 3D graptolite fragments were recovered from conodont residues from the basal Goéland Member of the Jupiter Formation (sample AI 649). One of the fragments could be assigned to *Climacograptus retroversus* (identified by Dr. D. J. Loydell), a common Aeronian graptolite.

Brachiopod faunas are abundant in the Anticosti Island succession and some are age diagnostic. Cocks & Copper (1981) reported an *Hirnantia* Fauna from 5.6 m below the O.P.B. on the eastern side of the island. However, Lespérance (1985) and Rong & Harper (1988) argued that the identifications presented were questionable and that the fauna could not be assigned to the *Hirnantia* Fauna with any confidence.

Jin *et al.* (1996, fig. 2) depicted the ranges of age-diagnostic brachiopods through the Silurian. *Virgiana barrandei* occurs in the upper Becscie Formation and *Virgiana mayvillensis* within the lower Merrimack Formation and indicate a Rhuddanian age. The first representative of *Pentamerus*, *Pentamerus* n. sp., occurs within the uppermost Gun River Formation and the basal Jupiter Formation and indicates correlation with the mid Aeronian. This is succeeded by *Pentamerus oblongus*, which occurs from the mid-Jupiter Formation (Richardson Member) to basal Chicotte

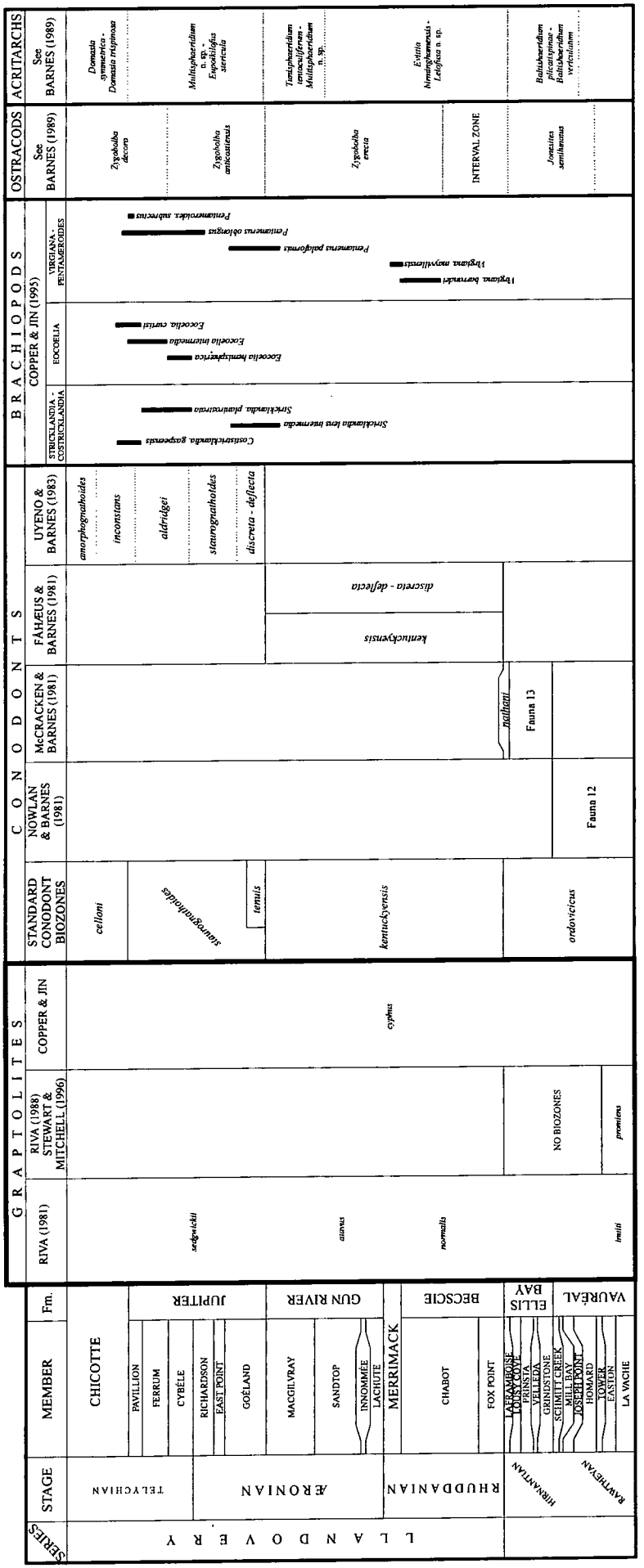


Figure 3.19 Summary of biostratigraphical data for Anticosti Island

Formation. The appearance of *Eocoelia curtisi* within the Pavillion Member and basal Chicotte Formation allows correlation with the early Telychian.

3.3.2b Microfauna

Micropalaeontological studies have included ostracodes (Copeland, 1981, 1982, 1983), acritarchs (Duffield & Legault, 1981; Duffield, 1985), and chitinozoa (Achab, 1981). The acritarch and ostracod biozonal schemes are summarised in Figure 3.19.

Conodont studies have been undertaken for the Vauréal (Nowlan & Barnes, 1981), Ellis Bay (McCracken & Barnes, 1981), Becscie, Merrimack, Gun River (Fåhræus & Barnes, 1981), Jupiter and Chicotte Formations (Uyeno & Barnes 1981, 1983). A conodont biozonal scheme has been proposed for the strata (Figure 3.19). Studies focusing on the conodont distribution across the Ordovician-Silurian boundary include McCracken & Barnes (1981), Barnes (1988) and Nowlan (1982).

Within this study, additional samples were collected across the Ordovician-Silurian boundary at Point Laframboise (AI 1; Figures 3.22 & 3.23), Cap à 1' Aigle (AI 2) and a spot sample from Lac Wickenden Road (AI 17a; Figures 3.20 & 3.21). Samples through the Silurian strata were mainly taken from levels that had not been previously sampled. These included the Merrimack Formation (Jupiter 24 Lodge, AI 3), the Gun River - Jupiter formational boundary (Dauphine River Road, AI 9; Sandtop Cliffs, AI 16), the East Point Member (Jupiter Formation; Dauphine River Road, AI 11c; Sandtop Road, AI 13) and the upper Chicotte Formation (Grand Lac Sale, AI 20; Brick River, AI 7; Figure 3.26). A detailed sampling through the upper Jupiter (Ferrum and Pavillion Members) and basal Chicotte Formations exposed at Brisants Jumpers was also undertaken (AI 5; Figures 3.24 & 3.25).

The Ellis Bay Formation yields a distinctive fauna (Fauna 13) dominated by *Gamachignathus* (McCracken & Barnes, 1981). In this study, the Lousy Cove Member has yielded *Gamachignathus ensifer* (up to 67%), *Gamachignathus hastatus* (up to 29%), *Oulodus robustus* (up to 43%), *Panderodus acostatus* (up to 61%; with serrate arcuatiform elements in sample AI 625), *Panderodus panderi* (up to 4%), *Phragmodus undatus* (up to 100%), *Pseudooneotodus beckmanni* (up to 2%),

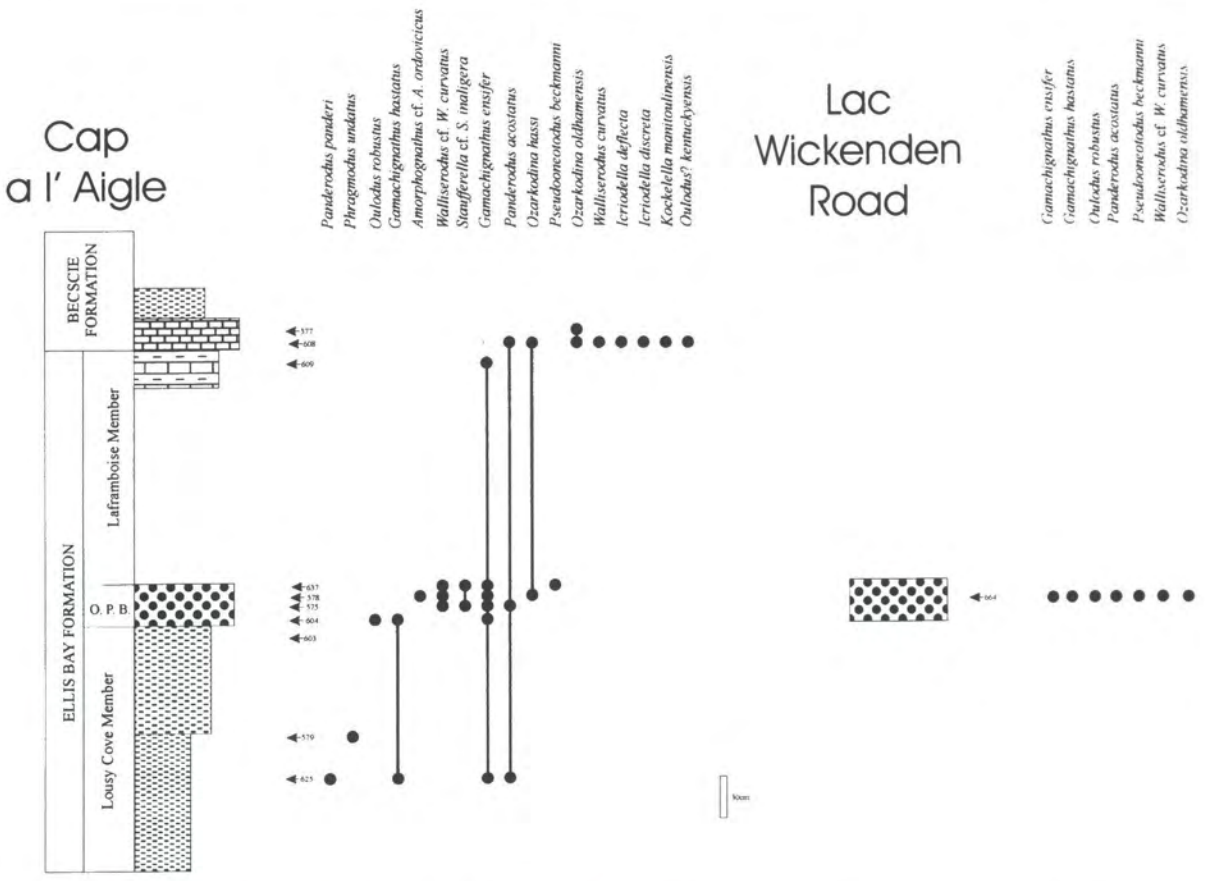


Figure 3.20 Conodont ranges through the Cap à l' Aigle section (Locality AI 2) and the Lac Wickenden Road grab sample (Stop AI 17a).

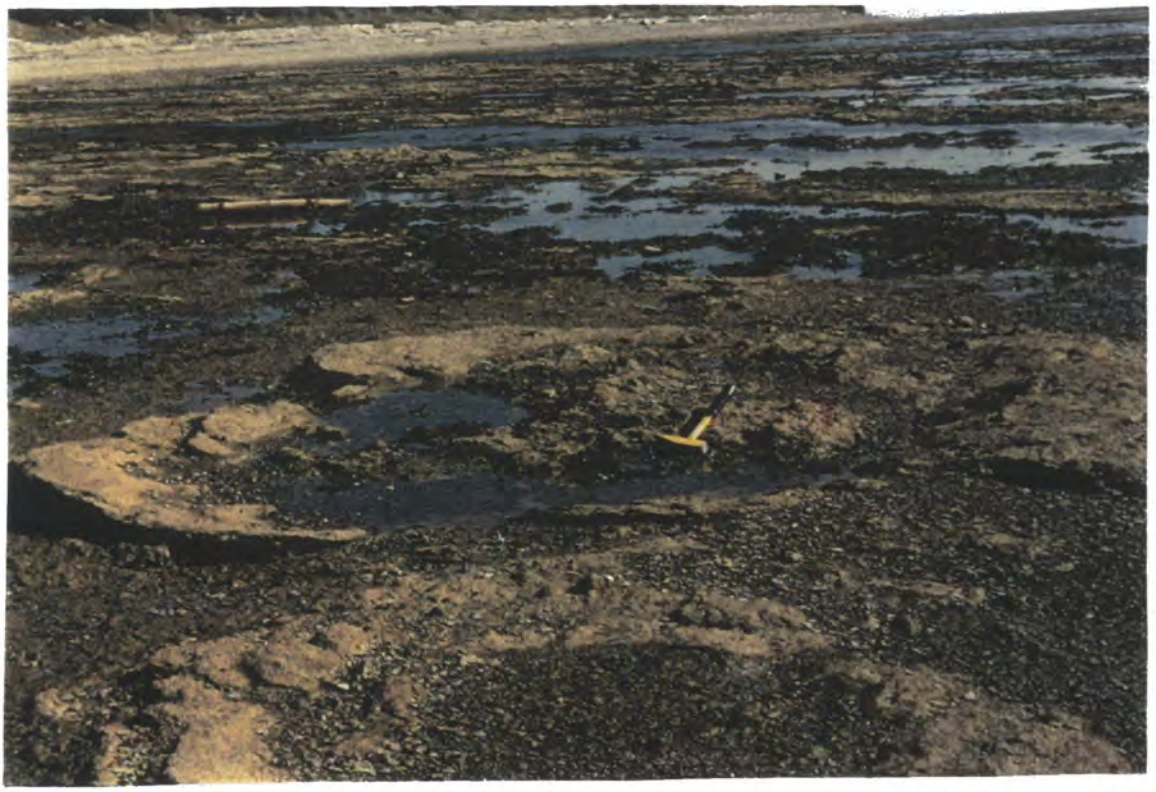


Figure 3.21 A bioherm exposed on the wave-cut platform at the Cap à l' Aigle section (Locality AI 2).

Walliserodus cf. W. curvatus (up to %), *Drepanoistodus suberectus* (up to 2%), and *Staufferella* cf. *S. inaligera* (up to 11%). A more diverse fauna was recovered from the section at Salmon River (eastern side of the island) studied by McCracken & Barnes (1981), which may reflect a slightly deeper-water environment (see Sami & Deroches 1992).

Samples from the O.P.B. have yielded *Gamachignathus ensifer* (up to 47%), *Gamachignathus hastatus* (up to 29%), *Oulodus robustus* (up to 43%), *Pseudooneotodus beckmanni* (up to 38%) and *Staufferella* cf. *S. inaligera* (up to 20%). Taxa that first appear within the O.P.B. include *Ozarkodina hassi* (up to 11%). *Walliserodus* cf. *W. curvatus* (up to 33%) and *Amorphognathus* cf. *A. ordovicicus* (11%) continue from older strata. Taxa that occurred with the O.P.B. continue into the overlying Bioherm Unit, apart from *Gamachignathus hastatus*. *Panderodus acostatus* (up to 14%; only in uppermost sample) and *Walliserodus cf. W. curvatus* (up to 29%) reappeared, and were joined by *Kockelella manitoulinensis* (50%), *Oulodus*? *nathani* (33%) and *Ozarkodina oldhamensis* (100%).

Panderodus acostatus (up to 42%), *Pseudooneotodus beckmanni* (up to 14%), *Kockelella manitoulinensis* (50%), *Oulodus*? *nathani* (33%), *Oulodus*? *kentuckyensis* (7%), *Ozarkodina hassi* (100%), *Decoriconus costulatus* (6%), and *Ozarkodina oldhamensis* (100%) continue into the Becscie Formation. Taxa that first appear within the Becscie Formation include *Walliserodus curvatus* (up to 30%) *Icriodella deflecta* (up to 25%) and *Icriodella discreta* (up to 4%).

Combining the data from this study and the studies of McCracken & Barnes (1981), Barnes (1988) and Nowlan (1982) indicates that all of the taxa within the Lousy Cove Member range up into the Laframboise Member apart from *Pseudobelodina dispansa, Pseudobelodina vulgaris*, *Panderodus liratus* and *Plegagnathus dartoni* (Barnes, 1988; Figure 4.9). Stepwise extinction of Ordovician species continued within the Laframboise Member and the basal beds of the Becscie Formation. *Aphelognathus* aff. *A. grandis*, *Oulodus ulrichi*, *Panderodus clinatus*, *Panderodus* cf. *P. staufferi* and *Plegagnathus nelsoni* have not been recorded from strata above the O.P.B. (herein, McCracken & Barnes, 1981, Barnes, 1988). *Amorphognathus ordovicicus*, *Gamachignathus hastatus*, *Oulodus robustus, Panderodus gibber* and *Walliserodus*

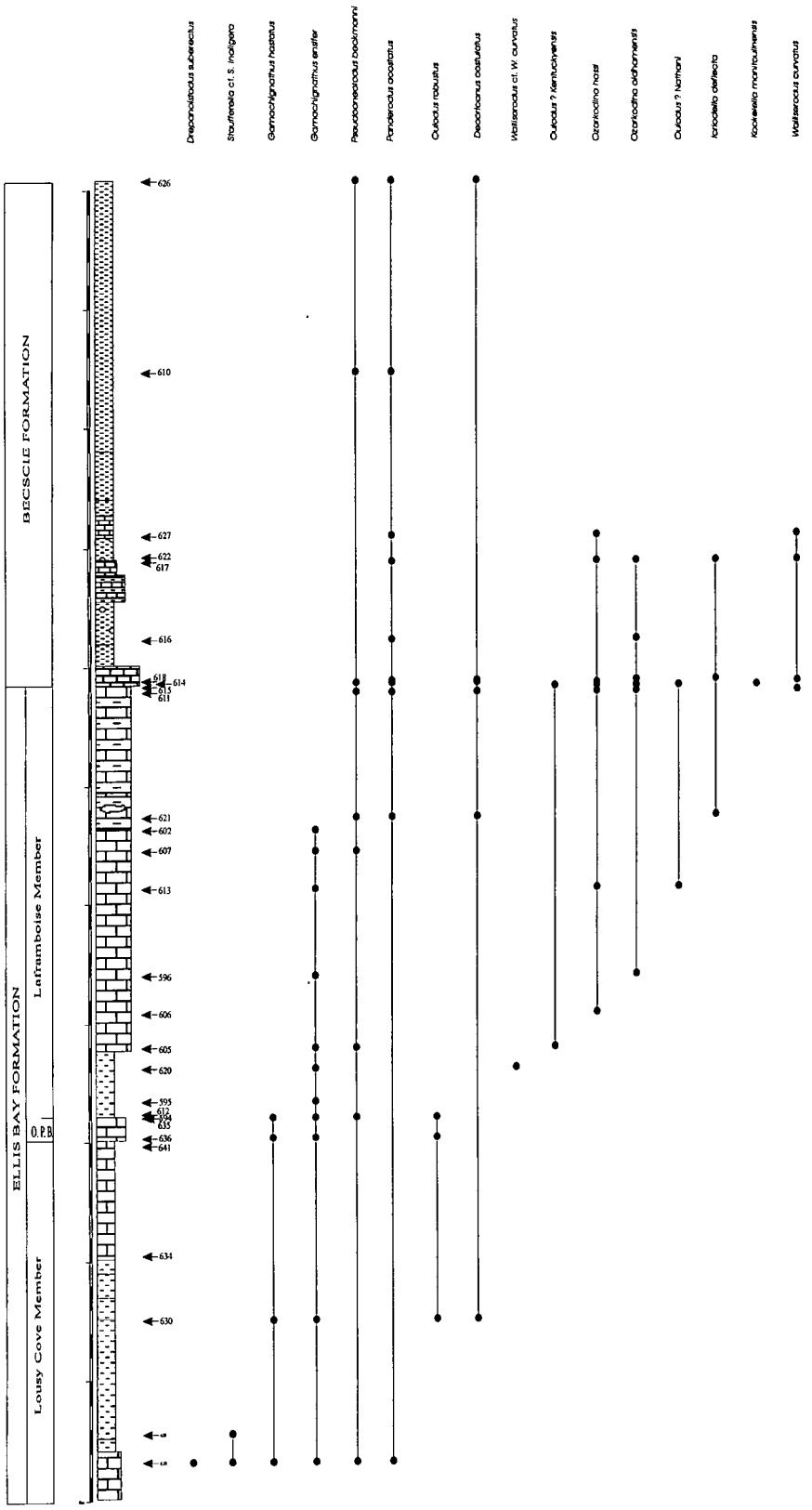


Figure 3.22 Conodont ranges through the Point Laframboise section (Locality AI 1). Each scale bar represents 20cm.

Figure 3.23 The Point Laframboise section (Locality AI 1). An exposure of the Lousy Cove Member of the Ellis Bay Formation overlain by the Becscie Formation.

Figure 3.24 The Brisants Jumpers locality (Locality AI 5): an exposure of the Ferrum and Pavillion Members of the Jupiter Formation, overlain by the Chicotte Formation.

cf. *W. curvatus* have not been recorded from above the Bioherm Unit (herein, McCracken & Barnes, 1981, Barnes, 1988). *Drepanoistodus suberectus, Gamachignathus ensifer, Oulodus rohneri, Phragmodus undatus, Pseudooneotodus mitratus* and *Staufferella inaligera* have not been recorded from the basal beds of the Becscie Formation (McCracken & Barnes, 1981, Barnes, 1988). The only species that were present within the Ordovician and continued above the basal Becscie Formation were *Decoriconus costulatus, Panderodus acostatus* and *Pseudooneotodus beckmanni* (Barnes, 1988).

McCracken & Barnes (1981) regarded the first appearance of a Silurian - type conodont taxon (i.e. *Ozarkodina oldhamensis* and hence the conodont-identified Ordovician - Silurian boundary), as occurring within the Bioherm Unit in sections around Ellis Bay (western end of the island). Later, Barnes (1988) recovered elements of *Ozarkodina oldhamensis* from the upper O.P.B. (below the Bioherm Unit) at Salmon River (eastern end of the island). However, he considered that the Ordovician - Silurian boundary should still be placed within the overlying Bioherm Unit in sections on the western end of Anticosti Island, as the O.P.B. thickened eastwards and may be in part equivalent to the Bioherm Unit. However, herein elements of *Ozarkodina* were recovered from the O.P.B. at Cap à 1' Aigle and Lac Wickenden Road on the western end of the island, thus suggesting that the base of the Transitional CBZ and the Ordovician-Silurian boundary (*sensu* McCracken & Barnes, 1981) lies within the upper O.P.B. (Laframboise Member).

Distomodus aff. D. kentuckyensis, Icriodella discreta, Kockelella manitoulinensis, Oulodus? kentuckyensis, Oulodus? nathani and *Walliserodus curvatus* first appear within the Bioherm Unit and continue into the Silurian (herein, McCracken & Barnes, 1981; Barnes, 1988). In summary, the first appearance of Silurian-type taxa is stepwise. The first appearance of *Ozarkodina* occurred within the O.P.B. in the Cap à l' Aigle section and in the sample from Lac Wickenden Road (Figure 3.20).

The first recorded appearance of a species of *Distomodus, Distomodus aff. D. kentuckyensis*, is within the Bioherm Unit (McCracken & Barnes, 1981; Barnes, 1988). However, Idris (1983) suggested that these elements should be re-classified within the genus *Icriodella*. McCracken & Barnes and Barnes (1988) did not recover

Distomodus kentuckyensis within the upper Ellis Bay Formation or within the lower Becscie Formation. Fåhræus & Barnes (1981) recovered *Distomodus* cf. *D. kentuckyensis* from the Becscie and Gun River Formations, but no elements identifiable as *Distomodus kentuckyensis*. Therefore, the base of the *kentuckyensis* CBZ can not yet be determined in the Anticosti Island section. Comparison with other sections indicates that an equivalent horizon to the base of *kentuckyensis* CBZ probably occurs within the lower Becscie Formation. Fåhræus & Barnes (1981) included the Becscie, Merrimack and Gun River Formations within the *kentuckyensis* CBZ.

Within this study, only the basal and uppermost strata of the Becscie Formation were sampled. Fåhræus & Barnes (1981) sampled throughout the Becscie Formation and recovered *Decoriconus costulatus*, *Distomodus* cf. *D. kentuckyensis*, *Icriodella deflecta*, *Oulodus*? *kentuckyensis*, *Ozarkodina hassi*, *Ozarkodina oldhamensis*, *Panderodus gracilis*, *Pseudooneotodus beckmanni*, and *Walliserodus curvatus*. The taxa had all continued from older strata apart from a number of taxa classified in open nomenclature, which include *Oulodus*? sp., *Ozarkodina* sp. A *Panderodus* spp. and *Pterospathodus* sp..

Samples from the uppermost Becscie Formation studied herein (AI 672 & AI 673) are dominated by *Panderodus acostatus* (up to 56%), *Oulodus* cf. *O. panuarensis* (up to 25%) and species of *Icriodella* (up to 25%). Other taxa include *Ozarkodina pirata* (up to 17%), *Ozarkodina protoexcavata* (5%: previously unknown from the island), and *Ozarkodina hassi* (3%). Samples from the overlying Merrimack Formation have yielded the same species as the samples from the uppermost Becscie Formation. *Ozarkodina oldhamensis* (up to 11%), *Oulodus*? *kentuckyensis* and one element possibly attributable to *Pseudolonchodina fluegeli* (1%) have also been recovered. The fauna is characteristic of the *kentuckyensis* CBZ.

In the Fåhræus & Barnes (1981) study, taxa that continued from the Becscie Formation into the Gun River Formation included *Decoriconus costulatus*, *Distomodus* cf. *D. kentuckyensis*, *Icriodella deflecta*, *Oulodus*? *kentuckyensis*, *Oulodus*? sp., *Ozarkodina oldhamensis*, *Ozarkodina* sp. A, *Panderodus gracilis*, *Pseudooneotodus beckmanni* and *Walliserodus curvatus*. Taxa that appeared within

the Gun River Formation included *Walliserodus sancticlairi*, *Ozarkodina* aff. *O. gulletensis*, *Ozarkodina* sp., and *Carniodus* cf. *C. carnulus* (=*Ozarkodina protoexcavata*). The current data suggests that *Oulodus*? *nathani*, *Ozarkodina hassi* and *Kockelella manitoulinensis* became extinct within the Becscie Formation. *Ozarkodina protoexcavata* has not been recovered from strata younger than the Merrimack Formation.

A sample (AI 751) from the Sandtop Member of the Gun River Formation collected herein, yielded *Panderodus acostatus* (80%), *Ozarkodina pirata* (17%), *Oulodus*? *kentuckyensis* (1%) and *Panderodus panderi* (1%). This fauna continued into the uppermost member of the Gun River Formation (Macgilvray Member) apart from *Oulodus*? *kentuckyensis*, which has not been recovered. Elements of a species of *Distomodus*, *Distomodus* sp. (10%), have been recovered from the Macgilvray Member, but the lack of well preserved Pa elements prevents specific identification. The lack of species of *Icriodella* in these samples indicates extinction within the Gun River Formation.

Taxa that continue from older strata into the basal Jupiter Formation (Goéland Member) include *Panderodus acostatus* (up to 78%), *Ozarkodina pirata* (up to 10%), *Panderodus panderi* (9%), *Distomodus* sp. (up to 5%), *Oulodus* cf. *O. panuarensis* (up to 6%), *Pseudooneotodus beckmanni* (up to 3%), *Walliserodus curvatus* (2%) and *Ozarkodina oldhamensis* (1%). *Panderodus staufferi* (up to 23%) is recorded for the first time in the succession. In the Uyeno & Barnes (1983) study, additional first appearances within the basal Goéland Member include *Pranognathus posteritenuis* (9%), *Pranognathus siluricus* (5%), *Pseudolonchodina fluegeli*, *Oulodus* sp. A and *Pseudooneotodus bicornis*? The samples from the Goéland Member were also dominated by coniform taxa (71%; *Decoriconus*, *Panderodus* and *Walliserodus*), *Ozarkodina pirata* (11%), *Pranognathus posteritenuis* (9%) and *Pranognathus siluricus* (5%). *Oulodus* cf. *O. panuarensis* and *Ozarkodina oldhamensis* are not been recorded in strata younger than the Goéland Member. The base of the *staurognathoides* CBZ and *tenuis* Sub-biozone occurs close to the base of the Jupiter Formation within the Goéland Member (Uyeno & Barnes, 1983).

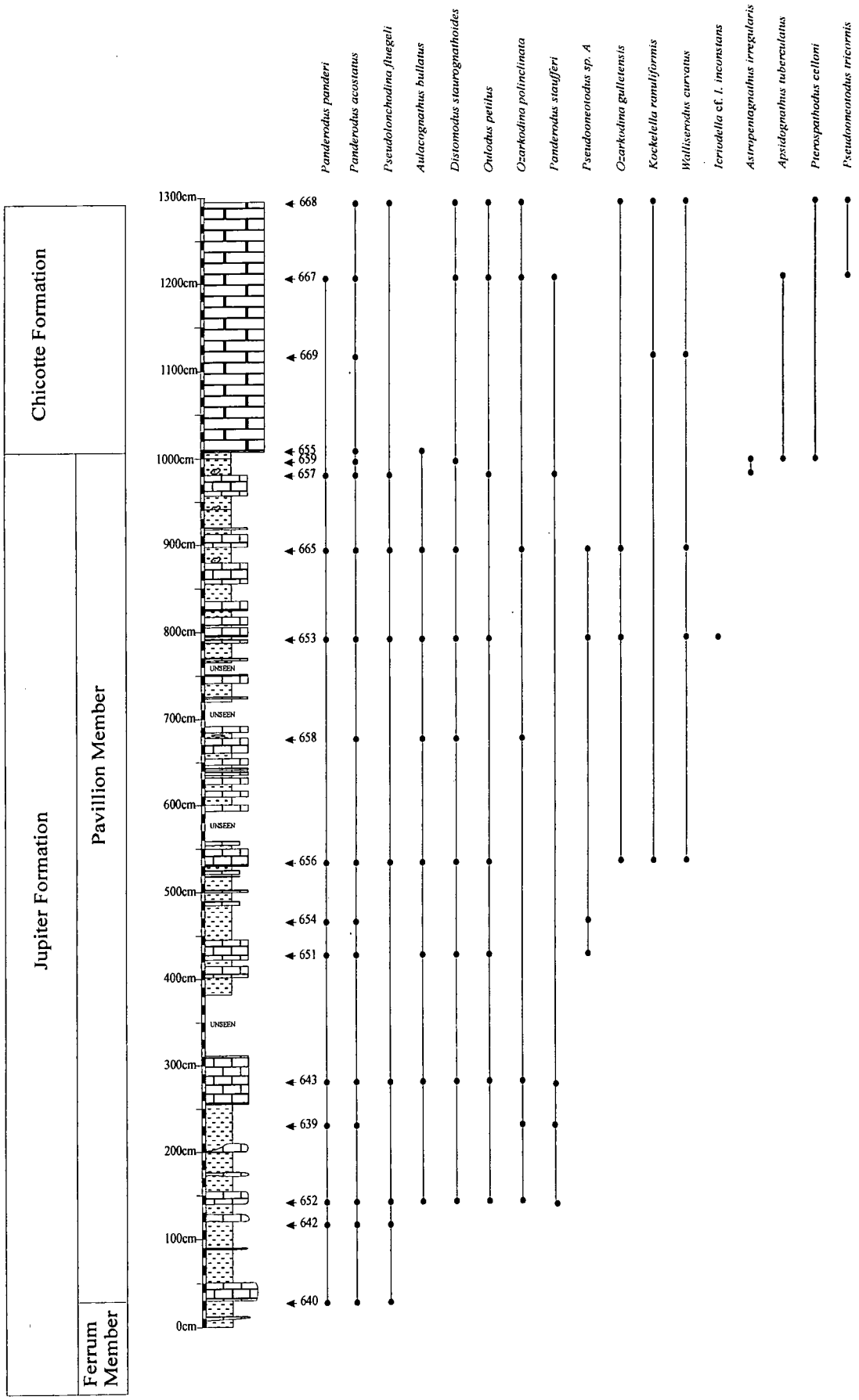


Figure 3.25 Conodont ranges through the Brisants Jumpers section (Locality AI 5).

The overlying East Point Member (not previously sampled for conodonts) yields taxa recovered from older strata. These include *Decoriconus fragilis* (3%), *Distomodus* cf. *D. staurognathoides* (<1%), *Oulodus* cf. *O. panuarensis* (<1%), *Ozarkodina pirata* (up to 50%), *Panderodus acostatus* (up to 71%), *Panderodus panderi* (2%), *Pseudooneotodus beckmanni* (<1%) and *Walliserodus curvatus* (up to 50%). These taxa appeared to become extinct in the upper East Point Member, as the overlying Richardson Member has only yielded rare *Panderodus* elements (Uyeno & Barnes, 1983). However, diversity increased again in the overlying, regressive Cybéle Member, which yields graptolites indicative of the *sedgwickii* GBZ (Riva, 1981). Taxa that continue from the beds below into the Cybéle Member include *Distomodus staurognathoides, Decoriconus fragilis*, *Ozarkodina pirata*, *Panderodus panderi*, *Panderodus unicostatus* (with serrate elements) and *Walliserodus sancticlairi* (Uyeno & Barnes, 1983). New taxa, which appeared in a stepwise pattern include *Ozarkodina* sp., *Dapsilodus obliquicostatus*, *Ozarkodina aldridgei* and *Icriodella* sp. (Uyeno & Barnes, 1983). This is the first appearance of *Dapsilodus obliquicostatus* in the Anticosti Island section. *Pranognathus posteritenuis* briefly reappears within one sample and does not reappear again in the section (Uyeno & Barnes, 1983).

Coniform taxa were dominant in the samples from the Cybéle Member. For example, coniform taxa comprised 91% of Sample AI 281 (Uyeno & Barnes, 1983). The only other taxa in this sample were *Ozarkodina aldridgei* 3% and *Ozarkodina pirata* 6% (Uyeno & Barnes, 1983). Coniform taxa comprise 78% of sample AI 292. Additional taxa include *Distomodus* cf. *D. kentuckyensis* (0.8%), *Oulodus* sp. B (5%), *Ozarkodina aldridgei* (13%) and *Pseudooneotodus bicornis* (3%; Uyeno & Barnes, 1983). *Ozarkodina pirata* has not been recovered from strata younger than the Cybéle Member.

A sample from the overlying Ferrum Member, collected herein, was dominated by *Panderodus acostatus* (55%) and *Panderodus panderi* (30%). Taxa that continued from older strata include *Pseudolonchodina fluegeli* (8%), *Ozarkodina aldridgei* (2%), *Walliserodus curvatus* (2%) *Distomodus staurognathoides* (1%), and *Decoriconus fragilis* (<1%). Taxa that are first recorded in this Member include *Oulodus petilus* (1.2%), *Ozarkodina* cf. *O. masurensis* (<1%) and *Oulodus* sp. B (<1%). *Ozarkodina aldridgei*, *Icriodella inconstans*, *Pseudooneotodus bicornis*,

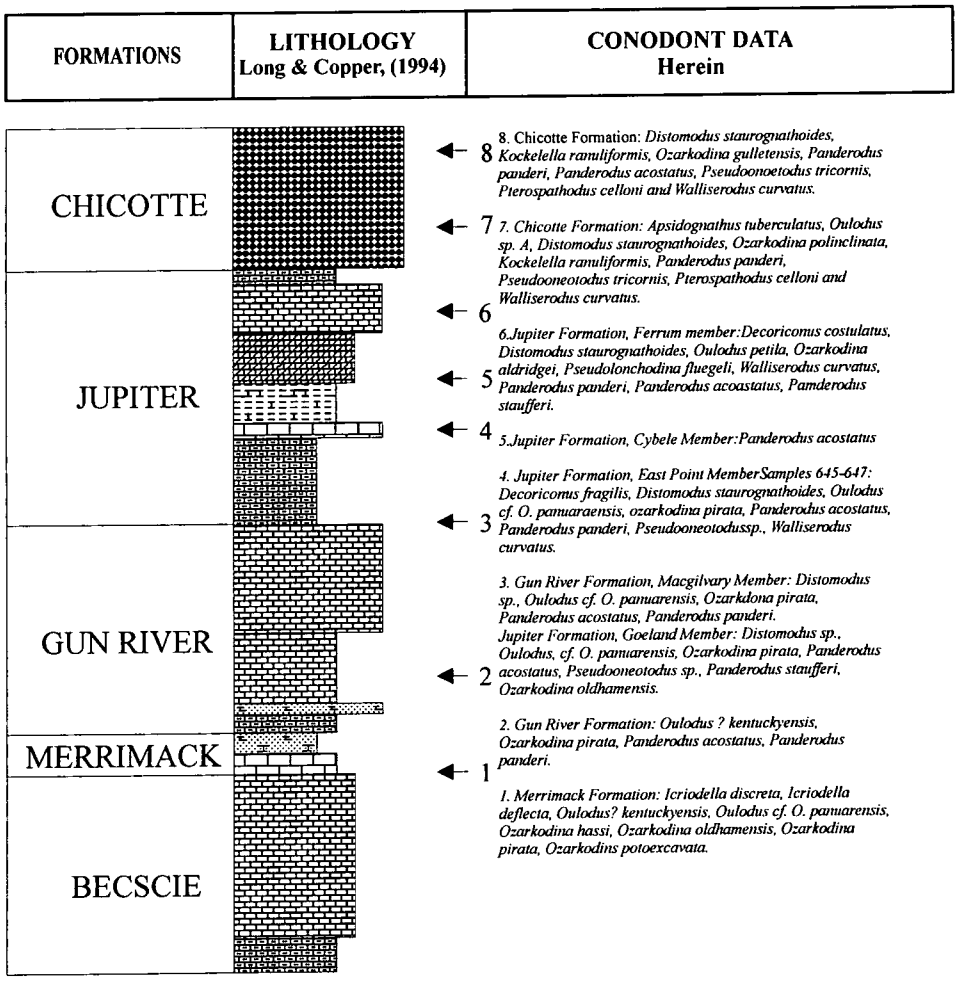


Figure 3.26 The occurrence of conodont species through the Llandovery strata on Anticosti Island.

Ozarkodina clavula, Astropentagnathus irregularis and *Aulacognathus bullatus* do not occur in strata younger than the Pavillion Member.

Taxa that continue from the Ferrum Member into the Pavillion Member include *Panderodus panderi* (up to 22%), *Panderodus acostatus* (up to 79%), *Pseudolonchodina fluegeli* (12% in basal sample), *Distomodus staurognathoides* (up to 21%), and *Oulodus petilus* (up to 9%). New taxa appear in a stepwise fashion through the Pavillion Member. These include *Ozarkodina polinclinata* (AI 652; up to 9%), *Aulacognathus bullatus* (AI 652; up to 17%), *Pseudooneotodus* sp. A (AI 654; up to 7%), *Ozarkodina gulletensis* (AI 656; up to10%), *Icriodella* cf. *I. inconstans* (AI 653; <1%), *Astropentagnathus irregularis* (AI 657; up to 19%), *Pterospathodus celloni* (AI 659; 7%) and *Apsidognathus tuberculatus* (AI 659; 7%). Uyeno & Barnes (1983) also recorded the presence of *Ozarkodina aldridgei, Walliserodus sancticlairi, Pseudooneotodus bicornis* and the first appearance of *Ozarkodina clavula* within the Pavillion Member.

Samples of the Chicotte Formation, from the Brisants Jumpers locality, were dominated by *Panderodus*: *Panderodus panderi* (up to 21%), *Panderodus acostatus* (up to 38%) and *Panderodus staufferi* (up to 23%). Other taxa that have continued from the Pavillion Member include *Distomodus staurognathoides* (up to 5%), *Kockelella ranuliformis* (up to 5%), *Oulodus petilus* (up to 3%), *Ozarkodina gulletensis* (2%), *Ozarkodina polinclinata* (10%), *Pseudolonchodina fluegeli* (up to 2%) and *Pterospathodus celloni* (up to 14%). *Walliserodus curvatus* (up to 10%) reappears and first appearances include *Kockelella ranuliformis* (up to 5%; AI 668) and *Pseudooneotodus tricornis* (up to 8%; AI 668). Younger samples of the Chicotte Formation at other localities additionally yielded *Ozarkodina excavata, Panderodus langkawiensis* and *Oulodus* sp.

Uyeno & Barnes (1983) reported a broken specimen indicating the occurrence of *Pterospathodus amorphognathoides* in the lower Chicotte Formation and thus assigned the upper part of the formation to the *amorphognathoides* CBZ. Their report has not been verified herein, and only elements of *Pterospathodus celloni* are present in samples from the Chicotte Formation and the identification of the element that they recovered is not conclusive.

In summary, the Transitional CBZ occurs within the Laframboise Member (Ellis Bay Formation). This is followed by the *kentuckyensis* CBZ, which extends through the Becscie and Gun River Formations. The *staurognathoides* CBZ occurs within the Jupiter Formation and *Pterospathodus celloni* first appears within the basal Chicotte Formation (Uyeno & Barnes, 1983; Herein).

3.3.3 Chemostratigraphy and sea-level cyclicity

3.3.3a Chemostratigraphy

The $\delta^{18}O$ and $\delta^{13}C$ ratios of carbonates within the Ellis Bay and Becscie Formations have been discussed by Orth *et al.* (1986), Long (1993), Brenchley *et al.* (1994) and Underwood *et al.* (1997). Long (1993) identified three to five periods of Oxygen isotope depletion through the upper Vauréal and Ellis Bay Formations and suggested that they were related to advances of the Gondwanan ice sheet (Figure 3.27).

A large negative $\delta^{13}C$ anomaly occurs at the top of the uppermost bed of the Lousy Cove Member (Underwood *et al.*, 1997) and is followed by a large positive excursion throughout the Laframboise Member. These data indicate that the Laframboise Member can be correlated with the glacial maximum, which has been defined by the presence of a positive $\delta^{18}O$ and $\delta^{13}C$ excursion in other sections (Orth *et al.*, 1986; Long, 1993; Underwood *et al.*, 1997; Section 1.7.1). The $\delta^{13}C$ ratio dropped to pre-excursion levels at the base of the Becscie Formation (Long, 1993; Underwood *et al.*, 1997) which Wang *et al.* (1995) suggested may indicate a biomass reduction. $\delta^{18}O$ and $\delta^{13}C$ studies through the Silurian strata have been limited to data for the Merrimack and Jupiter Formations (Brenchley *et al.*, 1994). The lack of a continuous record through the succession inhibits interpretation.

Trace element abundances and mineral content have been studied through the Anticosti Island strata by Orth *et al.* (1986) and Wang *et al.* (1995). A marked change in concentration of trace elements occurs between the Lousy Cove Member and the O.P.B., and has been interpreted as representing either an increase in the rate of

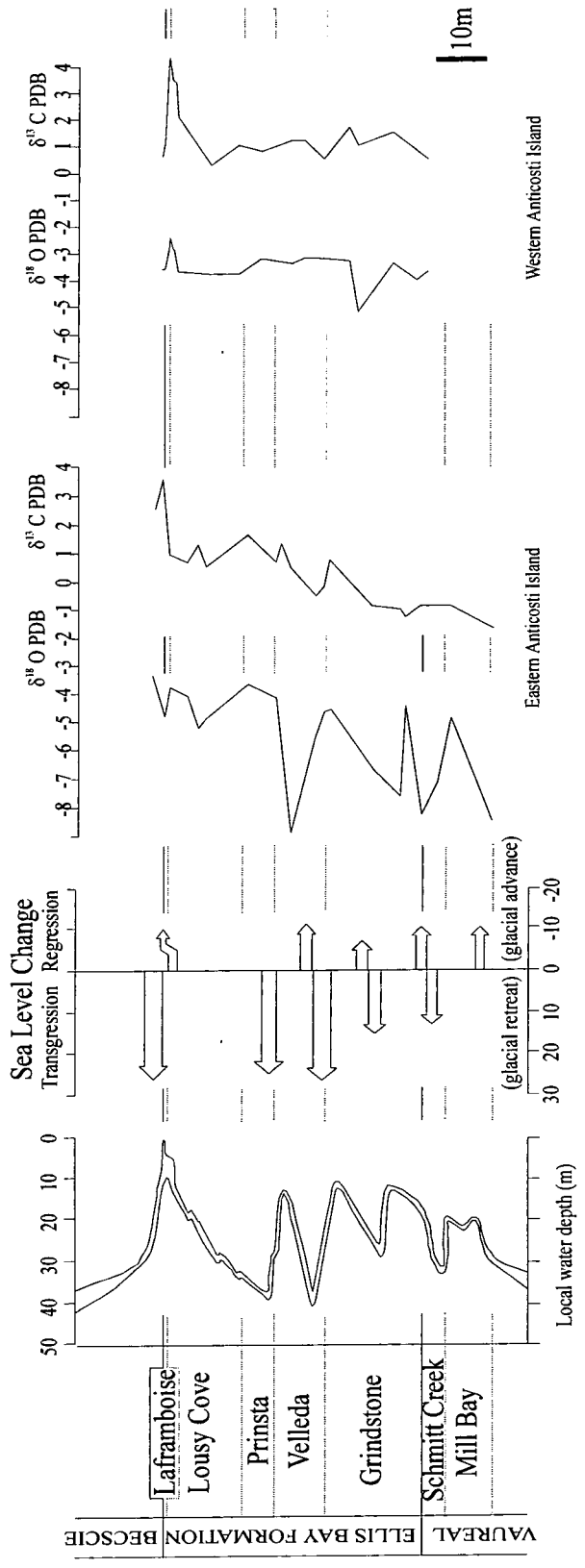


Figure 3.27 Oxygen and Carbon stable isotope data and sea-level variations through the upper Vauréal and Ellis Bay Formations, after Long (1993).

carbonate precipitation or a decrease in the input of detrital material (Orth *et al.*, 1986). Wang *et al.* (1995) suggested that higher Mg abundances in the Lousy Cove Member indicated slight dolomitisation, and high levels of Mn in the lowermost Becscie Formation indicated a change in palaeoredox conditions; the mobilisation of reduced Mn is thought to increase with increasing volume of anoxic water (Force *et al.*, 1983).

The abundances of most trace elements varies with the clay content of the sediments. For example, Orth *et al.* (1986) recorded an Ir anomaly coinciding with the first appearance of *Ozarkodina* (*sensu* McCracken & Barnes, 1981), resulting from increased clay content within that layer. An additional minor positive Ir anomaly on the upper surface and within the O.P.B. was identified and attributed to condensation and slower sedimentation rates associated with hardgrounds (Wang *et al.*, 1995).

The Llandovery $^{87}Sr/^{86}Sr$ curve published by Ruppel *et al.* (1996) was largely compiled using conodont specimens from the Jupiter and Chicotte Formations (Section 2.5). The interpretation of $^{87}Sr/^{86}Sr$ data has been discussed in Chapter 2 (Section 2.5). An increase in the ratio would accompany a sea-level fall, whereas a decrease in the $^{87}Sr/^{86}Sr$ ratio would occur during a sea-level rise. The four samples through the *staurognathoides* CBZ (Jupiter Formation) depict a general rise, with a fall in the uppermost part of the biozone. This correlates with the sea-level fall identified by Long (1996) through the Richardson, Cybéle and Ferrum Members, followed by a rise in the Pavillion Member. Two samples from the basal *celloni* CBZ (Chicotte Formation) illustrate an increasing trend, which indicates that this was a period of falling sea level.

3.3.3b Sea-level cyclicity

There have been many discussions regarding the sea-level fluctuations at different horizons within the Anticosti Island succession (e.g. Petryk, 1981b; Long, 1993; Diecchio, 1995; Long & Copper, 1994; Brunton & Copper, 1994; Sami & Deroches, 1992) and a number of sea-level curves have been constructed through the whole succession (e.g. Petryk, 1981a; Johnson *et al.*, 1981; Long, 1996). The stratigraphy of the island has been reviewed subsequent to the sea-level studies of Pertyk (1981a) and

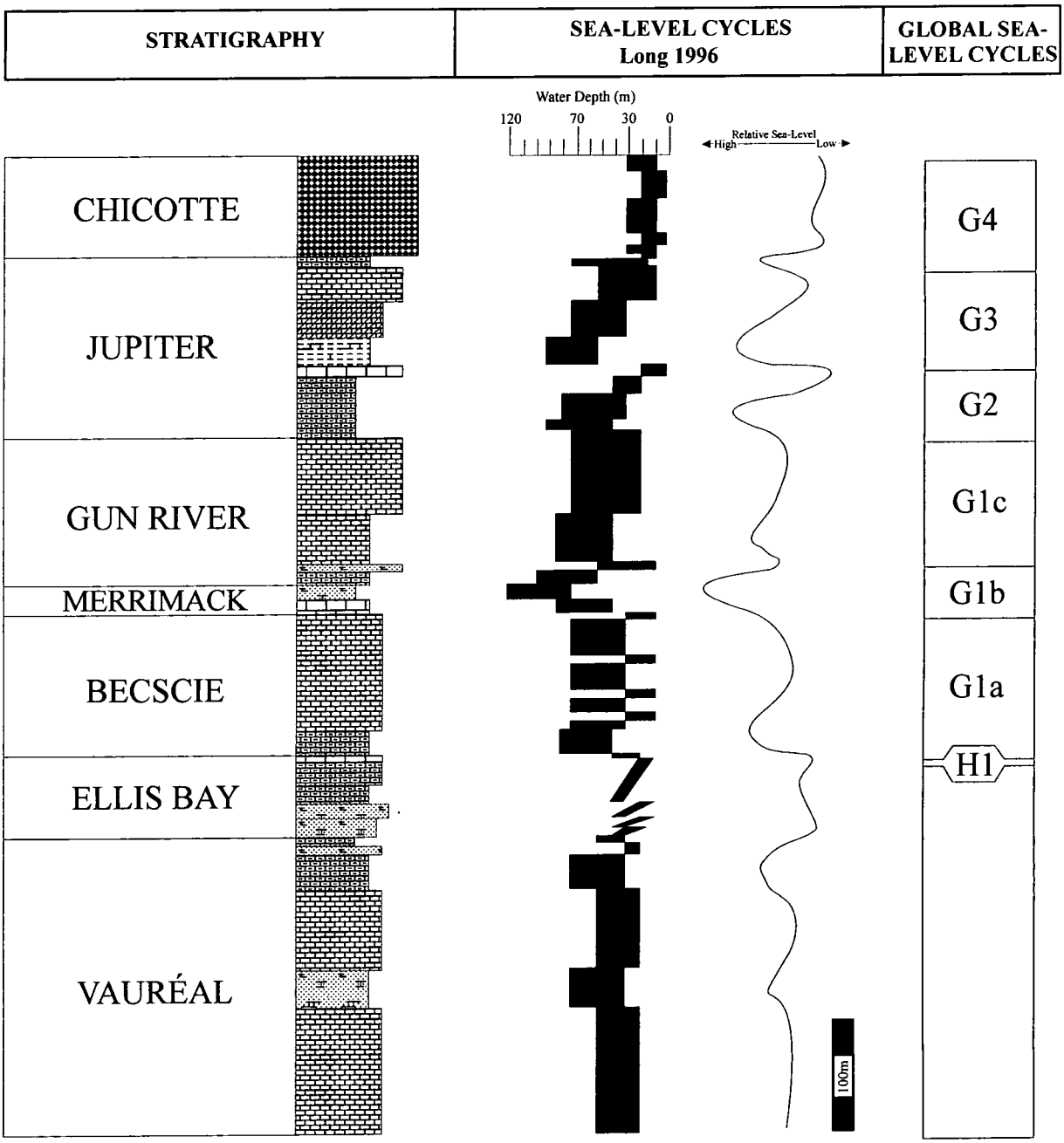


Figure 3.28 Sea-level cycles through the Anticosti Island succession from Long (1996) compared with the global sea-level cycles.

Johnson *et al.* (1981) and major advances have been made in the interpretation of the lithofacies. Consequently, the sea-level curve of Long (1996) is preferred herein (Figure 3.28). This curve was constructed using a combination of sedimentological and palaeontological data and identified two transgressive-regressive cycles in the Ordovician strata and six transgressive-regressive cycles within the Silurian strata.

There have been a number of discussions regarding the sea-level fluctuations across the end-Ordovician mass extinction event (Lousy Cove Member to basal Becscie Formation) (Lake *et al.*, 1981; Orth *et al.*, 1986; Long & Copper, 1987; Long, 1993; Brenchley *et al.*, 1994), but a detailed sea-level curve has yet to be published. Long (1993) recognised a regression starting in the Prinsta Member and culminating in the Laframboise Member. He estimated the change in water depth as a shallowing from 40m to 10m. Orth *et al.* (1986) suggested that the carbonates in the lower part of the Lousy Cove Member were deposited below wave base, whereas the uppermost bed represented shallowing to within the wave-affected zone.

The O.P.B. overlying the top of the Lousy Cove Member has been interpreted as being deposited in shallower and higher-energy water than the beds below (Lake, 1981; Orth *et al.*, 1986). Long (1993) regarded the presence of oncoids as indicating deposition in less than 10m of water, whilst Orth *et al.* (1986) suggested that the upper part of the O.P.B. was deposited in lower-energy conditions than the base.

Lake (1981) sub-divided the overlying Bioherm Unit into lower- and upper-mound facies. He regarded the lower-mound facies as being deposited in a quiet, shallow-subtidal environment, whereas the upper mound was deposited in slightly shallower, more-agitated conditions. This indicates a shallowing trend through the upper Bioherm Unit. The Bioherm Unit is overlain by a crinoidal grainstone (crinoid blanket), which Lake (1981) suggested had formed in a shallow, subtidal environment where there was considerable current or wave action, whilst Orth *et al.* (1986) suggested that it was deposited below wave base. Lake (1981) and Long (1993) noted that intertidal exposure might have occurred at the top of the bioherms, which would indicate that regression in the Bioherm Unit culminated in intertidal conditions.

There have been some reports of hiatuses within the upper Ordovician sections on Anticosti Island (Brenchley *et al.*, 1994; Underwood *et al.*, 1997). The multiple hardgrounds at the base of and within the O.P.B. (Lake, 1981), could reflect a significant time break (Long & Copper, 1994). However, there is a lack of marked blackening on the hardgrounds, which might have been expected if prolonged exposure had occurred (Long & Copper, 1994). Long & Copper (1994) noted that the basal beds of the Becscie Formation overlie a stepped erosional horizon on top of the bioherm and inter-bioherm sediments. They argued that this surface could either represent a period of emergence or erosion by wave-induced currents. The appearance of blackened surfaces and hardground borings are evidence of possible bacterial action in an intertidal to subtidal setting (Long, 1993).

Herein it is suggested that a general regressive trend occurs through the Lousy Cove Member, which culminates at the boundary between the Lousy Cove Member and the Laframboise Member. The subsequent transgression began in the O.P.B. and was followed by regression through the Bioherm Unit. The identification of a positive $\delta^{13}C$ excursion associated with this minor T-R cycle suggests correlation with Global Cycle H1 (Underwood *et al.*, 1997).

Within the overlying Llandovery strata, Long (1996) identified six sea-level cycles. The use of the well-constrained biostratigraphic framework for Anticosti Island allows the correlation of these cycles with the global cycles outlined in Chapter 2. The cycles within the Becscie Formation, Merrimack-lower Gun River Formation and the Gun River Formation can be correlated with Laurentian Cycles L1a-c. Laurentian Cycle L1a represents the initial major post-glacial transgression. The appearance of *Virgiana* within the Merrimack Formation, associated with a T-R cycle allows correlation with Laurentian Cycle L1b. The T-R cycle identified by Long (1996) within the Gun River Formation can be correlated with Laurentian Cycle L1c.

Three cycles occurred within the Jupiter Formation: Goéland to East Point Members, Richardson to Ferrum Members and within the Pavillion Member (Long, 1996). The appearance of *Pranognathus*, *Distomodus staurognathoides*, and *Pentamerus* associated with transgression in the Goéland Member (Jupiter Formation) allows

correlation with the base of Global Cycle G2. Global Cycle G3 occurs within the *sedgwickii-halli* GBZs, which have been correlated with the Richardson, Cybéle and Ferrum Members. Correlation of the Pavillion Member with Global Cycle G4a is suggested by appearance of *Eocoelia curtisi* and *Aulacognathus bullatus* within its transgressive base. The appearance of *Pterospathodus celloni* within the Chicotte Formation may indicate correlation with the transgressive base of Global Cycle G4b. However, a shallowing was identified at the base of the Chicotte Formation by Long (1996) followed by a subsequent rise. Therefore, this may only tentatively be correlated with G4b.

3.4 Outer Shelf: Prongs Creek, Northern Yukon Territories

The Prongs Creek section is situated in the northern Yukon Territorories (Figure 3.29). The sediments were deposited within the Selwyn Basin, at the edge of the Royal Mountain Platform adjacent to the Richardson and Blackstone Troughs.

A reconnaissance survey of the rocks at Prongs Creek was conducted by Norford (1964) and the area was mapped by Norris (1982). The section spans the Upper Ordovician and Llandovery, and is composed of three main lithological units. The Upper Ordovician platform limestones (Platformal Limestone Unit) are overlain by a transitional limestone (Transitional Limestone Unit). They are both considered to occur within the Whittaker Formation and are overlain by clastics of the Road River Group (Figure 3.32). The Road River Group has not been subdivided. The conodont samples and lithological descriptions for the section were provided by Dr. A. D. McCracken (Figure 3.30).

3.4.1 Lithology

The Upper Ordovician platformal limestones are light grey, resistant limestones containing silicified corals, crinoid ossicles, chert nodules, and pyrite. The overlying transitional limestone contains dark, argillaceous limestones, finely crystalline, dark limestones and minor shales. Brachiopods and trilobites are abundant. The overlying Road River Group is composed of fine-grained clastics with limestone interbeds.

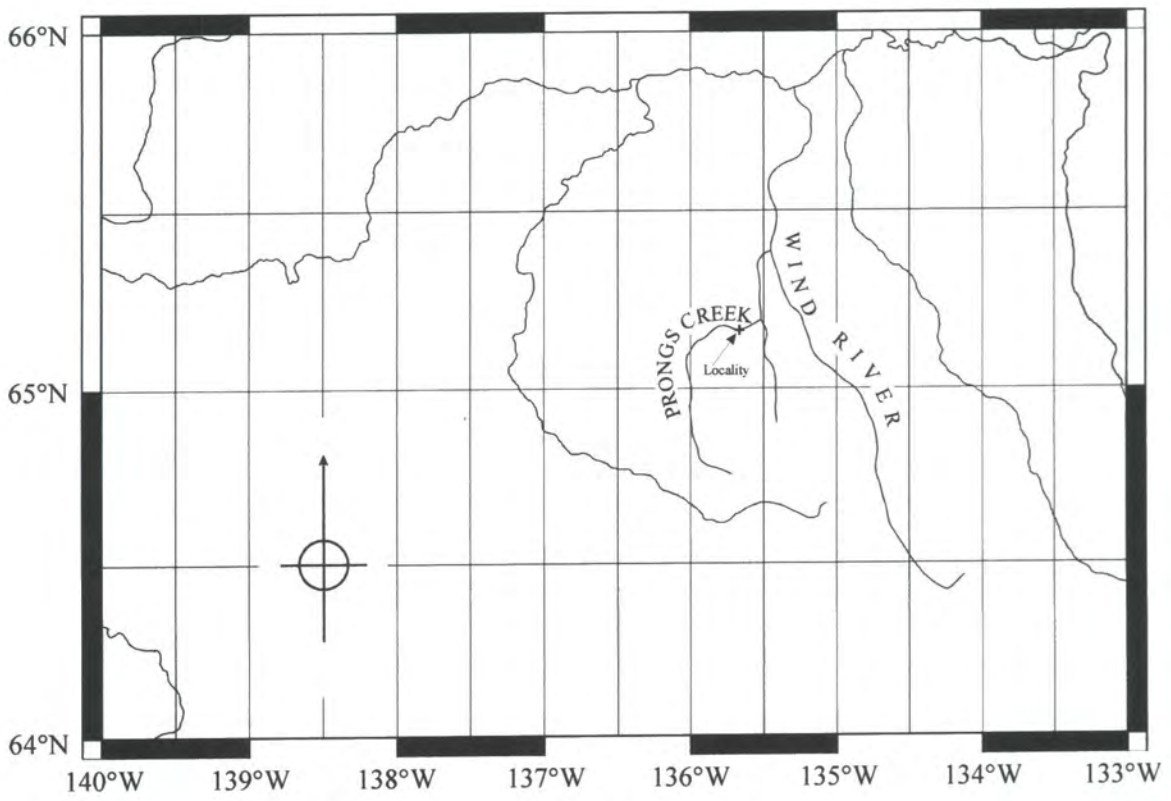


Figure 3.29 The location of the Prongs Creek section.

Figure 3.30 The Prongs Creek section. Photograph taken by A. D. McCracken.

Pyrite nodules and faint laminae are variably developed within the limestone interbeds. The group is largely unfossiliferous although graptolites occur at specific horizons.

3.4.2 Biostratigraphy

3.4.2a Macrofauna

Brachiopods, trilobites and graptolites from the Prongs Creek section were described by Raasch *et al.* (1961). However, it is not clear which part of the section the samples came from. The brachiopods and trilobites were probably recovered from the Transitional Limestone Unit. The brachiopods were juvenile or small and are not age diagnostic. Comparison of the trilobite fauna with faunas from Greenland led Raasch *et al.* (1961) to suggest a correlation with the *convolutus* GBZ. They recovered the graptolite *Monograptus turriculatus* (*turriculatus* GBZ), but did not state from which point in the section. Later, Norford (1964) recovered *turriculatus* and *spiralis* GBZs graptolites from 6-8m and 13.7-18.3m above the base of the Silurian section, respectively (Figure 3.32). This allowed the *turriculatus* (=*guerichi – turriculatus-crispus* GBZs) and *spiralis* GBZs to be placed within the Road River Group.

3.4.2b Microfauna

McCracken (1989) published a preliminary report on conodont samples collected throughout the succession, which are supplemented by further work carried out herein. This study has included 26 samples through the Transitional Limestone Unit and Road River Group (Figure 3.31).

Conodonts from the lower part of the Platformal Limestone Unit include *Aphelognathus*, *Juanognathus* and *Pseudobelodina* cf. *P. adentata* Sweet indicating a Maysvillian to Richmondian age (McCracken, 1989). Samples from the upper part of the limestone (46m and 61m) only yielded an undiagnostic fauna of *Panderodus* elements and one element of *Belodina* sp. This fauna indicates a broad Upper Ordovician age (McCracken, 1989).

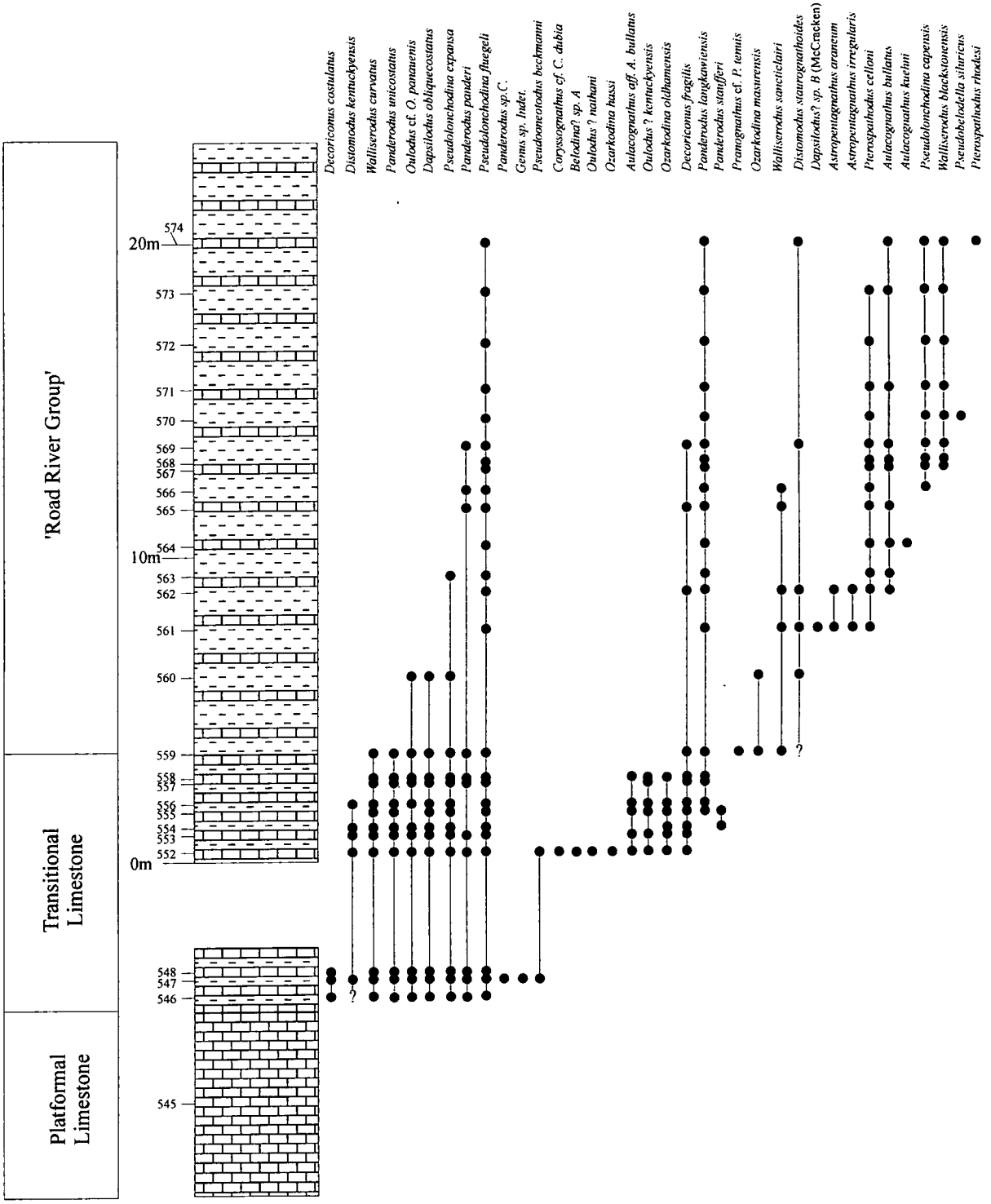


Figure 3.31 Conodont ranges through the Prongs Creek section.

The first sample (PC 546) that contains Silurian-type Taxa is dominated by *Panderodus unicostatus* (62%) and *Pseudolonchodina* sp. (14%). Other taxa include *Panderodus panderi* (9%), *Decoriconus costulatus* (5%), *Dapsilodus obliquicostatus* (3%), *Distomodus kentuckyensis* (3%), *Oulodus* cf. *O. panuarenis* (3%) and *Walliserodus curvatus* (1%). The taxa continue into younger strata (PC 547 and 548) and are joined by *Panderodus* sp. C (4%), Genus sp. Indet. (2%) and *Pseudooneotodus beckmanni* (1%) in sample PC 547. Samples PC 547 and PC 548 are dominated by *Pseudolonchodina* sp. (up to 37%). The fauna is indicative of the *kentuckyensis* CBZ.

Above a small gap in the record the Transitional Limestone Unit continues, and associated samples PC 552 to PC 558 are dominated by *Walliserodus curvatus* (up to 68%) and *Pseudolonchodina* sp. (up to 35%). *Dapsilodus obliquicostatus* increases in abundance with younging. *Corrysognathus* cf. *C dubia*, *Oulodus*? *nathani*, *Ozarkodina hassi*, *Pseudooneotodus beckmanni* and *Belodina* ? sp. A all occur within sample PC 552. They comprise less than 1% of the fauna, and are not seen in younger samples. Other taxa that first appear in sample PC 552, but continue through the Transitional Limestone Unit, include *Aulacognathus* cf. *A. bullatus* (less than 1%), *Decoriconus fragilis* (up to 9%), *Oulodus*? *kentuckyensis* (1%) and *Ozarkodina oldhamensis* (3%). The specimens of *Aulacognathus* recovered from the Transitional Limestone Unit represent the oldest recorded occurrence of that genus. *Panderodus staufferi* (PC 554) and *Panderodus langkawiensis* (PC 555) are the only species that first appear within the upper part of the Transitional Limestone Unit. *Aulacognathus* cf. *A. bullatus*, *Oulodus*? *kentuckyensis* and *Ozarkodina oldhamensis* have not been recovered above sample PC 558.

The uppermost carbonate bed, included within the Transitional Limestone Unit (sample PC 559) by McCracken (1989), yielded a fauna dominated by *Walliserodus curvatus* (44%) and *Dapsilodus obliquicostatus* (38%). Other taxa include *Ozarkodina masurensis* (7%), *Pranognathus* cf. *P. tenuis* (6%), *Oulodus* cf. *O. panuarensis* (3%), *Decoriconus fragilis* (2%), *Pseudolonchodina* sp. (2%) and *Panderodus unicostatus* (1%). *Panderodus panderi, Panderodus langkawiensis* and *Distomodus* cf. *D. kentuckyensis* each comprised less than 1% of the fauna. The presence of *Pranognathus* cf. *P. tenuis* and *Ozarkodina masurensis* indicates

correlation with the *tenuis* Sub-biozone. This is the first record of *Ozarkodina masurensis* outside Australia and the first record of *Pranognathus* from western Canada.

The lowest sample (PC 560) within the Road River Group yields *Pseudolonchodina fluegeli* (50%) and *Dapsilodus obliquicostatus* (38%). Other taxa include *Ozarkodina masurensis* (8%), *Distomodus* sp. (8%) and *Oulodus* cf. *O. panuarensis* (3%). This fauna lacks the index taxa of the standard conodont biozonal scheme, but its occurrence between the *tenuis* and *celloni* CBZs suggests comparison with the *staurognathoides* CBZ. *Dapsilodus obliquicostatus* (38%), *Ozarkodina masurensis* (8%) and *Oulodus* cf. *O. panuarensis* (3%) have not been recorded in younger strata.

At the base of the *celloni* CBZ (PC 561 & PC 562), the fauna is dominated by *Panderodus langkawiensis* (up to 33%) and *Pseudolonchodina* sp. (up to 57%). Age-diagnostic taxa include *Pterospathodus celloni* (up to 15%), *Astropentagnathus araneum* (1%), *Astropentagnathus irregularis* (up to 14%) and *Aulacognathus bullatus* (1%). Other taxa include *Decoriconus fragilis* (less than 1%), *Distomodus staurognathoides* (less than 1%) and *Walliserodus sancticlairi* (less than 1%). *Dapsilodus*? sp. B McCracken (2%), which was recovered from sample PC 561, has previously been recovered from the *gregarius* (=*triangulatus-pectinatus* to *argenteus* GBZs) and *turriculatus* GBZs (=*guerichi – turriculatus-crispus* GBZs) in the Canadian Cordillera (McCracken, 1991). It is the last representative of the Genus *Dapsilodus* in this section. The *celloni* CBZ continued through samples PC 563 to PC 573. The conodont species from the samples below continue through the *celloni* CBZ, apart from species of *Astropentagnathus* and *Dapsilodus. Aulacognathus kuenhi, Panderodus panderi, Pseudobelodella siluricus* appear within the *celloni* CBZ as does *Walliserodus blackestonenis*, which appears in sample PC 267 and becomes abundant (up to 53%).

The fauna recovered from Sample PC 574 is dominated by *Panderodus langkawiensis* (76%). Other taxa include *Pterospathodus celloni* (13%), *Pseudolonchodina* sp. (6%), *Walliserodus blackestonensis* (2%), *Aulacognathus bullatus* (1%) and *Distomodus staurognathoides* (less than 1%). Most importantly the fauna contains *Pterospathodus rhodesi* (1%), which is indicative of the *amorphognathoides* CBZ.

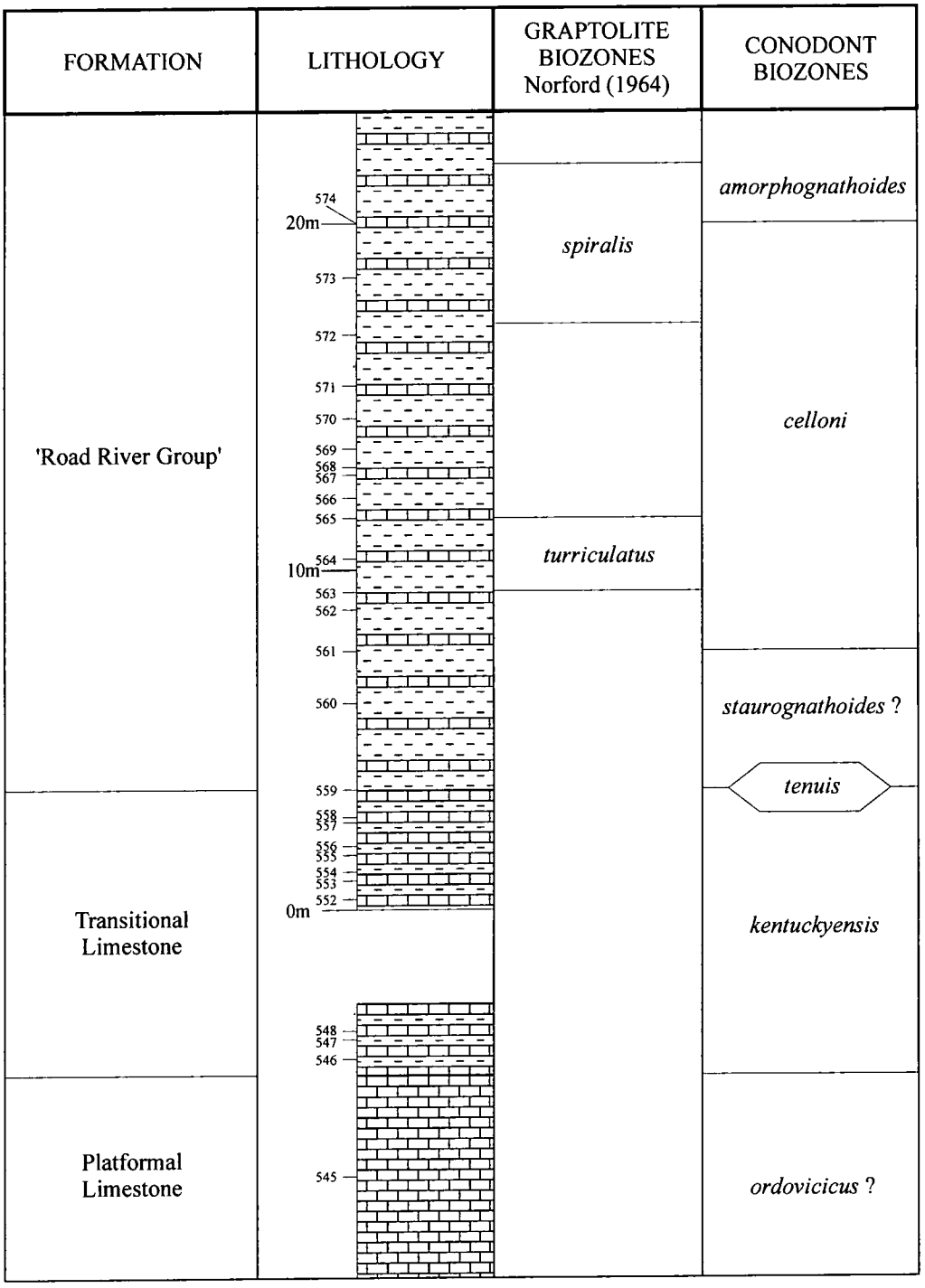


Figure 3.32 Summary of currently available biostratigraphical data for the Prongs Creek section.

In summary, the Transitional CBZ has not been identified in the Prongs Creek Section. The *kentuckyensis* CBZ extends through the Transitional Limestone Unit (sample PC 546 to PC 558) and the *tenuis* CBZ occurs in the uppermost bed of the Transitional Limestone Unit. The upper *staurognathoides* CBZ may be represented by the base of the Road River Group (sample PC 560). The bases of the *celloni* and the *amorphognathoides* CBZs occur within the Road River Group (sample PC 561and PC 574, respectively).

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3.4.3 Chemostratigraphy and sea-level cyclicity

There have been no published studies of the geochemistry or sea-level cyclicity for this section. However, a number of sea-level observations can be made. The glacial maximum can only be tentatively placed within the upper part of the Platformal Limestone Unit, as it represents the uppermost Ordovician. The transition between the Platformal Limestone Unit and the Transitional Limestone Unit can be interpreted as transgressive. It can be correlated with the post-glacial transgression (G1), as the *kentuckyensis* GBZ occurs at the base of the Transitional Limestone Unit. Transgression also occurred between the Transitional Limestone Unit and the Road River Group. This may be tentatively correlated with Global Cycle G3, as conodonts indicative of the *tenuis* GBZ occur within the uppermost bed of the Transitional Limestone Unit.

3.5 Summary

3.5.1 Correlation of the sections

The three sections vary in thickness, lithology and biostratigraphy (Figure 3.33), but can be correlated using the standard framework developed in Chapter 2 (Figure 3.34). Graptolite data is very limited for all three sections. Brachiopod data is useful for correlating the Lake Timiskaming and Anticosti Island sections, but not the Prongs Creek section. The conodont data discussed herein can help to correlate all three sections. The position of the global sea-level cycles (discussed in Chapter 2) within the three sections is discussed below.

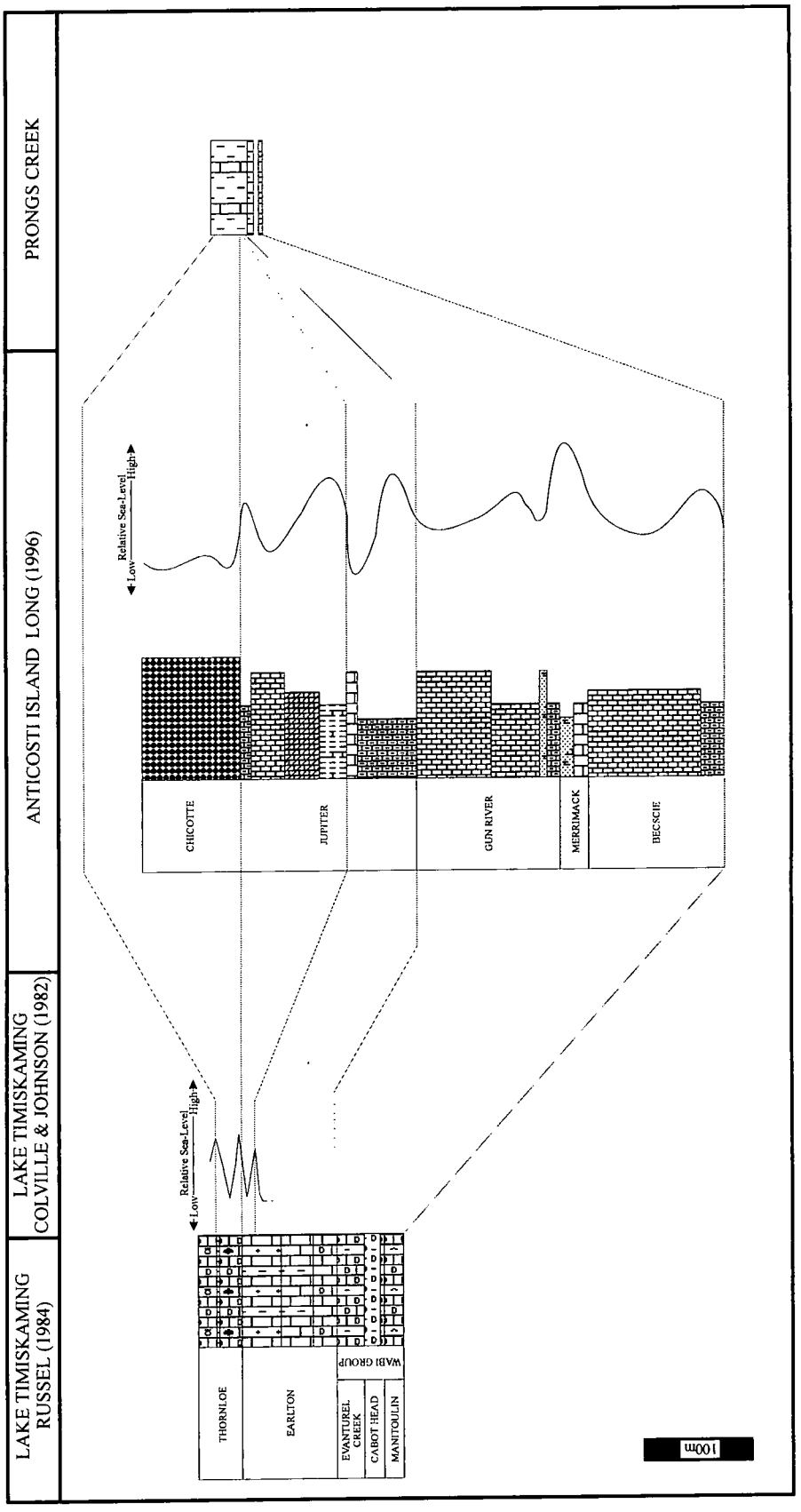


Figure 3.33 Comparison of the Lake Timiskaming, Anticosti Island and Prongs Creek sections.

Global Cycle H1 is a minor T-R cycle associated with the appearance of the *Hirnantia* Fauna and occurs within the *extraordinarius* GBZ (Fig 3.34). A positive $\delta^{18}O$ and $\delta^{13}C$ excursion indicates that this cycle occurs within the glacial maximum. On Anticosti Island, the *Hirnantia* Fauna has not been recovered, however, a positive $\delta^{18}O$ and $\delta^{13}C$ excursion associated with the minor T-R cycle within the Laframboise Member (Ellis Bay Formation) allows correlation with Global Cycle H1. Strata of this age are not exposed at Lake Timiskaming. This cycle can not be identified in the Prongs Creek section, but it is assumed that equivalent strata occur within the upper Platformal Limestone.

Global Cycle G1 represents the major post-glacial transgression and extends from the *persculptus* GBZ to the *argenteus* GBZ. The cycle spans the entirety of the *kentuckyensis* CBZ. It has been discussed in Chapter 2 that three cycles have been identified within Global Cycle G1 on Laurentia (L1a, L1b, L1c). Laurentian Cycle L1a extends from the *persculptus* GBZ to the *vesiculosus* GBZ and is associated with the basal part of the *kentuckyensis* CBZ. The base of Laurentian Cycle L1b occurs within the *cyphus* GBZ and is coincident with the appearance of the brachiopod genus, *Virgiana.* It has been identified on Anticosti Island within the Merrimack Formation, which bears *Virgiana.* Laurentian Cycle L1c occurs between *triangulatus-pectinatus* and *argenteus* GBZs and the upper part of the *kentuckyensis* GBZ, which can be correlated with the T-R cycle identified by Long (1996) within the Gun River Formation on Anticosti Island. All three cycles occur within the *kentuckyensis* CBZ. The *kentuckyensis* CBZ occurs within the Evanturel Creek Formation of Lake Timiskaming and the Transitional Limestone Unit at Prongs Creek, but sea-level fluctuations have yet to be discussed within those strata.

The transgressive base of Global Cycle G2 coincides with the first appearance of *Pranognathus tenuis* and / or *Distomodus staurognathoides.* It is associated with the *convolutus* GBZ and the first appearance of *Pentamerus* in shelf sections. The appearance of *Pranognathus*, *Distomodus staurognathoides* and *Pentamerus* associated with transgression in the Goéland Member (Jupiter Formation) on Anticosti Island, allows the base of Global Cycle G2 to be identified. The base of the

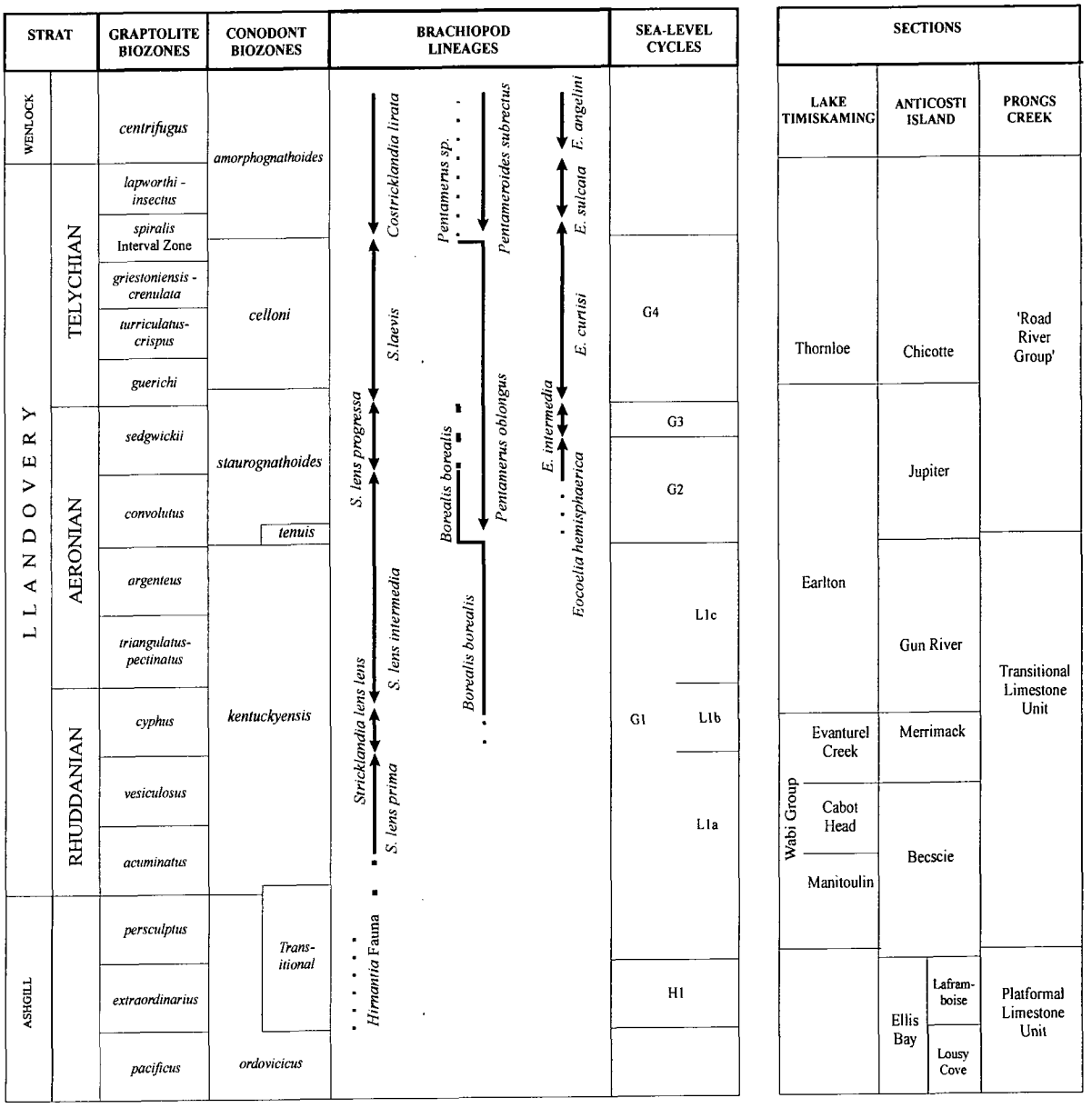


Figure 3.34 Correlation of the Lake Timiskaming, Anticosti Island and Prongs Creek sections with the standard framework.

staurognathoides-tenuis CBZ occurs within the uppermost Transitional Limestone Unit at Prongs Creek.

The upper regressive part of Global Cycle G2 is associated with the extinction of *Pranognathus* and a positive $\delta^{13}C$ isotope excursion in the basal *sedgwickii* GBZ (Wenzel, 1996; Heath *pers. comm.*). Shallowing within the East Point Member (Jupiter Formation) of Anticosti Island allows correlation of the regressive phase of Global Cycle G2.

Global Cycle G3 occurs within the *sedgwickii-halli* GBZs and in shelf settings it is associated with the presence of the brachiopods *Pentamerus oblongus*, *Stricklandia lens progressa* and *Eocoelia intermedia*. On Anticosti Island, the base occurs in the Richardson Member (Jupiter Formation), which is associated with transgression, and followed by regression through the Cybéle and Ferrum Members (Jupiter Formation).

The transgressive base of Global Cycle G4a coincides with the first appearance of *Aulacognathus bullatus* (in sections were it precedes the first appearance of *Pterospathodus celloni*). It may be correlated with the *guerichi* GBZ and the appearance of *Eocoelia curtisi* and *Stricklandia laevis* in shelf sections. On Anticosti Island, the first appearance of *Eocoelia curtisi* and *Aulacognathus bullatus* occurs within the transgressive base of the Pavillion Member (Jupiter Formation). It has not been identified in Lake Timiskaming or Prongs Creek.

The base of Global Cycle G4b occurs within the *turriculatus* GBZ and is marked by the first appearance of *Pterospathodus celloni* (*celloni* CBZ). The occurrence of *Eocoelia curtisi* and a species of *Pterospathodus*, within the Upper *Pentamerus* Bed (Thornloe Formation) of the Lake Timiskaming section suggests correlation with Global Cycle G4b. On Anticosti Island, a shallowing was identified at the base of the Chicotte Formation by Long (1996) followed by a subsequent rise. This may tentatively be correlated with G4b. The part of the Road River Group (sample PC 573) of Prongs Creek can be correlated with Global Cycle G4b, as the *celloni* CBZ occurs in these strata.

The transgressive base of Global Cycle G5 occurs within the *spiralis* GBZ, and is associated with the first appearance of *Pterospathodus amorphognathoides*. *Pentameroides* may also first appear during this episode, although the diachronous nature of its first appearance has been demonstrated (Colville & Johnson, 1982; Section 2.3.3). At Lake Timiskaming, the presence of *Coststricklandia multilirata* within the *Pentameroides* Bed (Thornloe Formation) suggests correlation with the Global Cycle G5. The base of the *amorphognathoides* GBZ occurs within the Road River Group (sample PC 574) at Prongs Creek.

The lithology, biostratigraphy and sea-level cyclicity have been discussed in the three sections, which are from differing palaeoenvironmental settings. This has enabled correlation of the sections, and the identification of the global sea-level cycles within the sections. The pattern of conodont extinction and recovery related to the end-Ordovician mass extinction event can now be studied and compared in these three disparate sections.

3.5.2 Variation in conodont faunas

It has been discussed in Section 1.6.2 that distinctive conodont biofacies occurred within the Upper Ordovician and Lower Silurian. Shelf and Slope Biofacies have been differentiated. The Shelf Biofacies is dominated by *Aphelognathus*, *Oulodus*, *Pseudobelodina*, *Plectodina* and *Phragmodus* in the Upper Ordovician, and *Panderodus,* in association with *Distomodus*, *Icriodella*, *Kockelella*, *Oulodus*, and *Ozarkodina* in the Llandovery. In the Upper Ordovician, the Slope Biofacies was dominated by *Dapsilodus* and *Periodon,* and in the Lower Silurian the dominant taxa included *Pseudolonchodina*, *Dapsilodus*, *Walliserodus*, *Decoriconus* and *Panderodus*. A number of sub-biofacies were identified by Sweet & Bergström (1984) within the Shelf Biofacies of the Upper Ordovician. .A Shelf-edge Biofacies dominated by *Amorphognathus* was also identified in the Upper Ordovician.

Anticosti Island is the only one of the three sections for which there is a good record of the Upper Ordovician taxa. The Ordovician strata include the Vauréal and Ellis Bay Formations. The Vauréal Formation was sampled for conodonts by Nowlan &

Barnes (1981). The conodont fauna is dominated by *Drepanoistodus suberectus*, and *Panderodus gracilis* (50-60%; Nowlan & Barnes, 1981). Other taxa include species of *Amorphognathus*, *Belodina*, *Phragmodus*, *Plectodina*, *Plegagnathus*, *Aphelognathus* and *Oulodus* (Nowlan & Barnes, 1981). Nowlan & Barnes (1981) identified three 'conodont ecozones': *Phragmodus*, *Amorphognathus* - *Plectodina* and *Oulodus* - *Aphelognathus*, which inhabited deep-subtidal to shallow-subtidal environments, respectfully. These ecozones may be equivalent to the *Phragmodus undatus*, *Plectodina* and *Aphelognathus-Oulodus* Biofacies of Sweet & Bergström (1984), respectively, thus, indicating that the depth-related biofacies continued into the lower Richmondian.

Within the overlying Ellis Bay Formation, McCracken & Barnes (1981) identified a number of conodont 'communities'. Community A was dominated by *Gamachignathus* (~45%) and *Panderodus gracilis* (~45%). The rest of the fauna comprised species of *Panderodus*, *Amorphognathus*, *Aphelognathus*, *Drepanoistodus*, *Oulodus*, *Phragmodus*, *Pseudooneotodus* and *Walliserodus*. Community B was dominated by species of *Panderodus* (65%). Non-coniform taxa comprised only 25% of the fauna. Community C was a low abundance fauna, composed of *Aphelognathus*, *Panderodus* and other coniform taxa. The non-coniform taxa seen in the other communities were 'essentially absent'. McCracken & Barnes (1981) suggested that Community A inhabited more offshore environments and Community C more nearshore environments. The three communities can not be related to any of the biofacies defined by Sweet & Bergström (1984), perhaps indicating that the shelf biofacies that they described no longer existed during the upper Richmondian.

Llandovery conodont samples have been collected from all three sections, which allows the conodont faunas in three different environments to be compared and contrasted. Rhuddanian and Aeronian samples from the Lake Timiskaming and Anticosti Island sections are dominated by species of *Ozarkodina, Oulodus,* and *Icriodella.* In the Telychian, *Aulacognathus* and *Pterospathodus* were also dominant. The fauna in both sections are characteristic of the Llandovery Shelf Biofacies. However, they differ in that *Panderodus* is dominant within the majority of the Anticosti Island samples, but not within the Lake Timiskaming samples, where it only

reached a high percentage (29%) within the Earlton Formation. Thus, variations did occur within the Shelf Biofacies.

The most dominant taxa in the Prongs Creek section vary through the strata and include *Panderodus, Walliserodus, Pseudolonchodina, Decoriconus* and *Dapsilodus*. Within the *kentuckyensis* CBZ, dominant taxa include *Dapsilodus obliquicostatus*, *Decoriconus costulatus*, *Panderodus unicostatus*, *Pseudolonchodina* sp. and *Walliserodus curvatus*. In the overlying *staurognathoides* CBZ, *Dapsilodus* and *Walliserodus* are the dominant taxa, but *Pseudolonchodina* regains its dominance within sample PC 560. Within the *celloni* CBZ, *Panderodus langkawiensis*, *Pseudolonchodina and Pterospathodus* can be dominant, with *Walliserodus blackestonesis* becoming dominant higher in the *celloni* CBZ. Within the *amorphognathoides* CBZ, *Panderodus* (*Panderodus langkawiensis*) and *Pterospathodus* are the dominant genera. This is an example of the Llandovery Slope Biofacies, which is dominated by *Pseudolonchodina.*

This variation in dominance seen through the Prongs Creek section may explain why different workers have identified different taxa as dominant within the Slope Biofacies. Armstrong (1990) described the 'slope and outer-shelf biofacies' as being composed of *Dapsilodus*, *Decoriconus* and *Pseudolonchodina,* whilst Watkins & Kuglitsch (1997) described an 'Offshore Biofacies' dominated by *Panderodus* (58%), *Pseudolonchodina* (13%) and *Walliserodus* (9%), whilst that of McCracken (1991b) was also dominated by *Dapsilodus* (15%).

The conodont genera had preferred environments, within which they reached an acme. However, they did occur within other environments, but in lower numbers. For example, *Pseudolonchodina* occurs within the Shelf Biofacies on Anticosti Island, but is much less common than in the Slope Biofacies of Prongs Creek. It reaches a maximum percentage of 12 within the basal Pavillion Member. Likewise, genera that are common in the Lake Timiskaming and Anticosti Island samples also occur in the Prongs Creek samples but in low numbers. The biofacies represented in the Lake Timiskaming and Anticosti Island samples are typical of biofacies found in Shelf Biofacies. In contrast, the biofacies represented by the Prongs Creek samples is typical of Slope Biofacies.

Chapter 4

The pattern and mechanisms of conodont extinction during the end-Ordovician mass extinction event

Chapter 4

The pattern and mechanisms of conodont extinction during the end-Ordovician mass extinction event

4.1 Introduction

At the end of the Ordovician, one of the most striking conodont extinction events in their 400 million year history occurred, thus terminating an episode of maximum conodont diversity (Sweet, 1985; Barnes & Bergström, 1988). Extinction occurred gradually through the Ashgill followed by a short, intense, interval of extinction in the latest Ashgill (Barnes & Bergström, 1988). The exact timing of the latest Ashgill extinction events has been difficult to determine and although linked to the glaciation, the actual causal mechanisms are uncertain.

Evidence from the Cornwallis Island section, which yields both graptolites and conodonts, suggests that two phases of extinction occurred, the first within the upper *pacificus* GBZ related to the start of the glacial maximum, and the second within the *acuminatus* GBZ during the post-glacial transgression (Melchin *et al.*, 1991). Graphical correlation of the Cornwallis Island section, with mid- to outer-shelf settings on the margins of Laurentia, led Armstrong (1995) to suggest that the major conodont extinction event occurred in the upper '*bohemicus* GBZ' (Section 2.3.1 & 2.3.4) at the end of the glacial maximum. Relic Ordovician taxa became extinct in the lower *acuminatus* GBZ, following the return to greenhouse conditions (Figure 4.1). The slight variation in the estimates of the timing of conodont extinction between the Melchin *et al.* (1991) and Armstrong (1990) studies suggests that either there are problems with the correlation of sections or that spatial differences occurred in the timing of conodont extinction events.

The pattern of conodont extinction has been studied herein on the mid-shelf section at Anticosti Island (Québec) and an outer-shelf section at Prongs Creek (Yukon).

Comparison of the pattern of extinction with biostratigraphical, sedimentary and geochemical data in each section and with sections from varying palaeoenvironments in the literature has enabled the timing, causal mechanisms and spatial variations in the extinction of conodonts within the Upper Ordovician to be determined.

4.1.1 Timing and correlation of the Upper Ordovician glacial maximum

The end-Ordovician mass extinction event is thought to have resulted from the initiation (1st strike of extinction) and cessation (2nd strike of extinction) of the glacial maximum (Brenchley *et al.*, 1995). The glacial maximum has been identified by sedimentological and isotopic data within the uppermost *pacificus* to upper *extraordinarius* GBZs in graptolitic sections (Underwood *et al.*, 1997; Armstrong & Coe, 1997). In shallow-water successions, the glacial maximum has been identified within strata bearing the *Hirnantia* Fauna and is constrained by $\delta^{13}C$ and $\delta^{18}O$ positive excursions (Brenchley *et al.*, 1994). In sections that have not been subject to geochemical analysis, the base of the glacial maximum may be identified at the point of maximum regression, and its end by the post-glacial transgression which occurred within the *persculptus* GBZ (Brenchley *et al.*, 1995). A minor transgressive-regressive cycle has been identified within Hirnantian strata and hence during the glacial maximum in North America (Global Cycle H1; see Section 2.4). On Anticosti Island (Québec), a positive $\delta^{13}C$ excursion is recognised within Global Cycle H1, supporting the view that there was a minor transgression within the glacial maximum.

4.1.2 Upper Ordovician conodont faunas

Conodont biofacies within the Upper Ordovician have been documented by Sweet & Bergström (1984; Section 1.6.2). Within the *velicuspis* Chron (Maysvillian), they identified a number of depth-related biofacies in sections marginal to Laurentia (Figure 4.4). They were not certain whether the biofacies were applicable to earlier and later periods. This thesis is concerned with the timing of the end-Ordovician mass extinction event and recognising spatial variations in the effect of the mass extinction event. Therefore, it is essential to identify whether the biofacies existed immediately

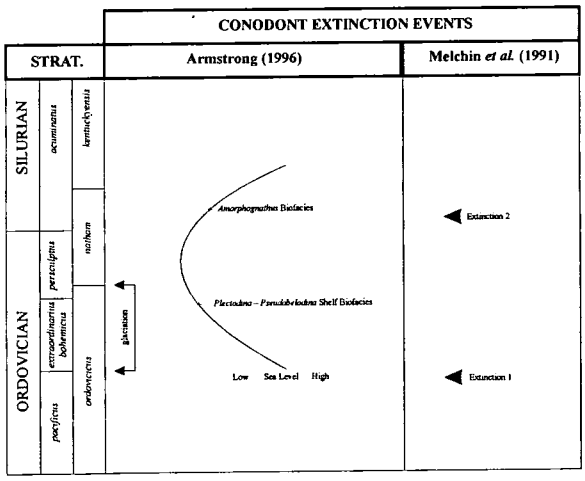


Figure 4.1 Conodont extinction events associated with the end-Ordovician glacial maximum identified by Armstrong (1996). After Armstrong (1996).

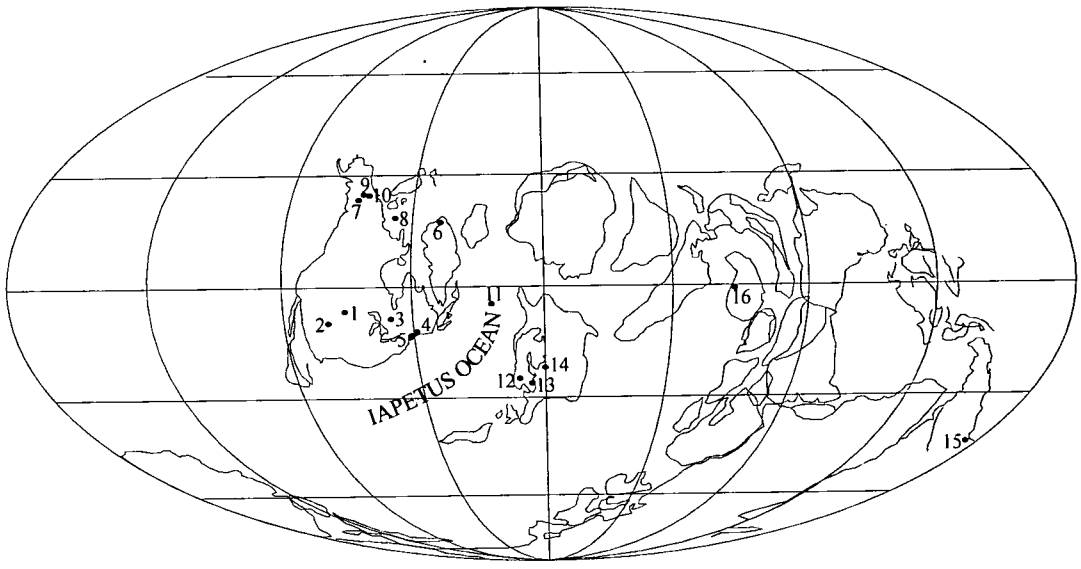


Figure 4.2 Palaeogeographic map showing the location of well studied Ordovician - Silurian boundary sections. Sections in Laurentia include: 1 = Missouri (McCracken & Barnes, 1982), 2 = Oklahoma (Barrick, 1986), 3 = Lake Timiskaming, Ontario (herein), 4 = Anticosti Island, Québec, 5 = Gaspe, Québec (Nowlan, 1981; Lespérance, 1985), 6 = J.P. Koch Fjord and Børglum Elv, Greenland (Armstrong, 1990), 7 = Avalanche Lake, Northwest Territories (Nowlan *et al.*, 1988; Wang *et al.* 1993), 8 = Cornwallis Island, Canadian Arctic (Melchin *et al.*, 1991), 9 = Prongs Creek, northern Yukon Territories (herein), 10 = Richardson & Blackstone Troughs (Lenz & McCracken, 1982) and 11 = Dob's Linn, Scotland (Barnes & Williams, 1988; Armstrong & Coe, 1997; Underwood *et al.*, 1997). Sections on Baltica include: 12 = Central Sweden (Marshall & Middleton, 1990), 13 = Motala region, Sweden (Bergström & Bergström, 1996), and 14 = Baltic States (Brenchley *et al.*, 1994). Other sections include: 15 = Argentina (Marshall *et al.*, 1997), 16 = Yichang, Hubei Province, China, (Wang *et al.*, 1993). Map modified from Nowlan *et al.*, (1997).

prior to the mass extinction event. In order to identify conodont biofacies in the uppermost Ordovician the composition of conodont faunas in different palaeoenvironments needs to be determined.

In the uppermost Ordovician, Laurentia was situated within the tropics (McKerrow & Scotese, 1990) and was surrounded by extensive basins, stretching from very shallow water to deep troughs (Figure 4.2, 4.3). Conodont data through Laurentian Upper Ordovician sections are available from a variety of different palaeoenvironments (Figure 4.2). Inner-shelf sections have been sampled in Oklahoma (Amsden & Barrick, 1986), Missouri (McCracken & Barnes, 1982) and Greenland (Armstrong, 1990). The sections on Anticosti Island and in the Perce region are believed to be examples of mid-shelf sections (Québec; Nowlan & Barnes, 1981). Outer-shelf sections occur at Avalanche Lake (north-west Canada; Nowlan *et al.*, 1988) and Cornwallis Island (Canadian Arctic, Melchin *et al.*, 1991). Basin and trough sections occur at Dob's Linn (Scotland; Barnes & Williams, 1988) and in the Selwyn Basin (north west Canada; Lenz & McCracken, 1982) sections.

Sweet & Bergström (1984) identified a number of biofacies in Upper Ordovician shelf sections, which will be regarded as sub-biofacies of the Shelf Biofacies, herein. They include the *Aphelognathus-Oulodus* (*Aphelognathus* and *Oulodus* = >40%), *Pseudobelodina* (*Pseudobelodina* = 20%), *Plectodina* (*Plectodina tenuis* = >40%) and *Phragmodus undatus* Sub-biofacies (Figure 4.4). In the inner-shelf sections of Missouri, the Hirnantian Noix Limestone (Sample 7159) yields a conodont fauna that is dominated by *Plectodina tenuis* (39%), *Aphelognathus grandis* (30%) and *Plectodina florida* (19%; McCracken & Barnes, 1982). The abundance of *Aphelognathus* and *Plectodina* within this fauna may indicate that the *Aphelognathus-Oulodus* and *Plectodina* Sub-biofacies continued in the uppermost Ordovician. However, in comparison the Hirnantian Keel Formation of an inner-shelf section in Oklahoma (Section M17, Sample 1) yields a fauna dominated by *Dapsilodus*? *mutatus* (29%), *Noixodontus girardeauensis* (24%), *Panderodus gracilis* (14%), *Decoriconus costulatus* (13%) and *Eocarniodus*? sp. (12%; Amsden & Barrick, 1986). The abundance of *Dapsilodus* in this inner-shelf section contradicts the Sweet & Bergström (1984) study, which indicated that *Dapsilodus* was only abundant in very deep water.

In the mid-shelf section on Anticosti Island, 'ecozones' possibly equivalent to the *Phragmodus undatus*, *Plectodina* and *Aphelognathus-Oulodus* Biofacies of Sweet & Bergström (1984) were identified within the Vauréal Formation (Nowlan & Barnes, 1981; Section 3.5.2), thus, indicating that the depth-related biofacies continued into the Lower Richmondian. Within the overlying Ellis Bay Formation, McCracken & Barnes (1981) identified three conodont 'communities', which were dominated by *Gamachignathus* (~45%) and *Panderodus gracilis* (~45%), *Panderodus* (65%) and a low-abundance fauna (*Aphelognathus*, *Panderodus* and other coniform taxa). The three communities can not be related to any of the biofacies defined by Sweet & Bergström (1984), which perhaps indicates that they no longer existed in mid-shelf settings during the Upper Richmondian.

In summary, the composition of the Shelf Biofacies in the uppermost Ordovician is very variable. Inner-shelf faunas can be compared with those described by Sweet & Bergström (1984) earlier in the Ordovician. However, in mid-shelf settings the faunas do not closely resemble those described by Sweet & Bergström (1984). In general, the faunas on the shelf were dominated by ramiform taxa, such as *Plectodina*, *Aphelognathus*, and *Oulodus*, and the coniform genus *Panderodus*. Variations in the Shelf Biofacies did occur. For example, genera that are locally dominant include *Gamachignathus* in mid-shelf sections and *Noixodontus* in inner-shelf sections.

An *Amorphognathus superbus - ordovicicus* Biofacies was identified at the shelf edge in the *velicuspis* Chron by Sweet & Bergström (1984). They included five sections as examples of the *Amorphognathus* Biofacies (table 1). Elements of *Amorphognathus* comprised 16-63%, and *Panderodus gracilis* 30%, of the fauna. *Plectodina* and *Phragmodus* could also be abundant reaching 27% and 19% of the fauna, respectively. The fauna comprised 24 species, eight of which were non-coniform taxa. The remaining coniform taxa include species of *Pseudobelodina*, *Plegagnathus*, *Panderodus*, *Belodina*, *Drepanoistodus*, *Dapsilodus*, *Staufferella*, *Protopanderodus* and *Coelocerodontus*.

Uppermost Ordovician shelf-edge sections that have been sampled for conodonts include those at Avalanche Lake (Nowlan *et al.*, 1988), and Cornwallis Island (Melchin *et al.*, 1991). At Avalanche Lake, the most dominant taxa included

Panderodus gracilis (44%), *Plectodina tenuis* (13%), *Pseudobelodina? dispansa* (11%), *Panderodus rhamphoides* (8%) and *Paraoistodus* (7%; Sample 46; Nowlan *et al.*, 1988). Other taxa include species of *Belodina*, *Besselodus*, *Coelocerodontus*, *Decoriconus*, *Drepanoistodus*, *Oulodus*, *Plegagnathus*, *Protopanderodus*, *Scabbardella*, *Staufferella* and *Walliserodus*. Additional genera that have been recovered from other uppermost Ordovician samples include *Aphelognathus*, *Juanognathus*, *Ozarkodina*, *Phragmodus*, *Pseudooneotodus*, and *Spinodus*. One element assignable to *Amorphognathus* has been recovered, *Amorphognathus* ? sp., but no elements assignable to *Amorphognathus ordovicicus* have been found.

Conodont abundance tables have not been published for uppermost Ordovician sections on Cornwallis Island, so the percentages of each species within the fauna can not be determined. Within the *pacificus* GBZ, the diverse Ordovician fauna was composed of coniform species plus *Amorphognathus ordovicicus* and *Plectodina* sp.. Common taxa between this fauna and the *Amorphognathus* Biofacies include *Belodina*, *Coelocerodontus*, *Panderodus*, *Plectodina*, *Plegagnathus*, *Protopanderodus*, and *Pseudobelodina.* Additional taxa include *Besselodus sp.*, *Pseudooneotodus mitratus*, *Scabbardella altipes* and *Walliserodus amplissimus* (Melchin *et al.*, 1991).

The fauna recovered from shelf-edge sections differs from that described by Sweet & Bergström (1984) in lacking *Amorphognathus* and *Phragmodus*. Similarities between the fauna described by Sweet & Bergström (1984) and that found in the uppermost Ordovician include the high diversity of coniform taxa and the dominance of *Plectodina* and *Panderodus* (i.e. Avalanche Lake section). Genera that the shelf-edge faunas from the Upper Ordovician and the uppermost Ordovician have in common include *Belodina*, *Coelocerodontus*, *Panderodus*, *Plectodina*, *Plegagnathus*, *Protopanderodus* and *Pseudobelodina.* Additional taxa that are found in both the Avalanche Lake section and the Cornwallis Island section include *Besselodus, Pseudooneotodus*, *Scabbardella* and *Walliserodus.*

The deeper-water *Dapsilodus mutatus* - *Periodon grandis* Biofacies of Sweet & Bergström (1984) was identified close to the Carbonate Compensation Depth (CCD). The fauna was dominated by *Dapsilodus mutatus* (38%) and *Periodon grandis*

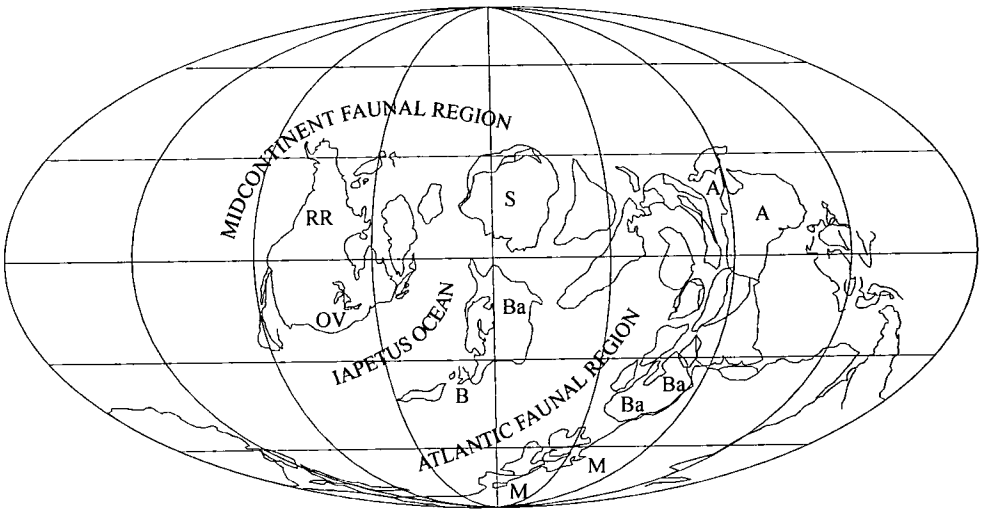


Figure 4.3 Palaeogeography of the Upper Ordovician and the distribution of conodont faunal regions, after Nowlan *et al.* (1997). The Midcontinent Faunal Region includes the Red River (RR), Ohio Valley (OV), Siberian (S) and Australasian (A) Provinces. The Atlantic Faunal Region comprises the Baltic (Ba), British (B), and Mediterranean (M) Provinces.

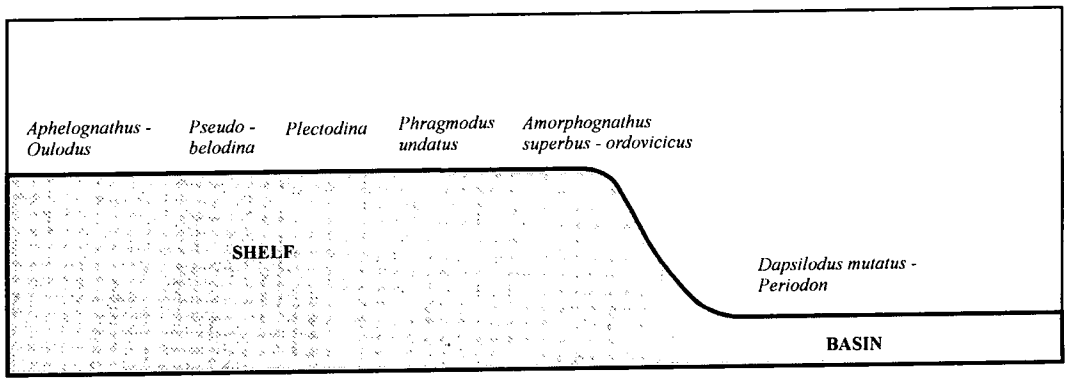


Figure 4.4 Depth related conodont biofacies identified during the *velicuspis* Chron. From Sweet & Bergström (1984).

(18%). The example discussed by Sweet & Bergström (1984) comprised 19 species (table 1). The non-coniform taxa represented included *Plectodina tenuis* (18%), *Phragmodus undatus* (<1%), *Icriodella superba* (<1%), *Amorphognathus ordovicicus* (1%), and *Rhodesognathus elegans* (<1%). The coniform taxa recovered comprise those included within the '*Amorphognathus*' Biofacies (except *Plegagnathus*), plus *Culumbodina.*

Uppermost Ordovician slope and trough sections that have been sampled for conodont include the Dob's Linn and Selwyn Basin sections. Faunas equivalent to the *Dapsilodus mutatus* - *Periodon grandis* Biofacies have been identified in these sections. The fauna recovered from the *pacificus* GBZ in the Trough sections of the Selwyn Basin is similar to that found in shelf-edge sections. For example, the fauna from sample PR 452.6M studied by McCracken (1987) was dominated by *Panderodus gracilis* (19%), *Scabbardella altipes* (18%) and *Protopanderodus insculptus* (13%). Non-coniform taxa comprise only 6% of the fauna and include *Amorphognathus ordovicicus* (3%), *Gamachignathus ensifer* (1%), *Oulodus ulrichi* (1%) and *Plectodina tenuis* (1%). Coniform taxa that occur within this section and the *Amorphognathus* Biofacies of Sweet & Bergström (1984) include species of *Belodina*, *Drepanoistodus*, *Panderodus*, *Protopanderodus* and *Pseudobelodina.* Additional taxa in this section include species of *Besselodus*, *Eocarniodus*, *Paraoistodus*, *Strachanognathus* and *Walliserodus.*

In the basinal Dob's Linn section, the taxa recovered from the *anceps* (= *pacificus*) GBZ include *Amorphognathus*, *Protopanderodus*, *Scabbardella* and *Hamarodus* (Barnes & Williams, 1988). Unfortunately, conodont abundance tables have not been published for this section, and so the structure of the fauna can not be determined. However, it can be observed from the list of fauna that it is markedly different from the *Dapsilodus mutatus* - *Periodon grandis* Biofacies of Sweet & Bergström (1984).

All of the faunas discussed above were recovered from the margins of Laurentia. Uppermost Ordovician - Silurian strata have been identified on other palaeocontinents, but few sections have been sampled for conodonts (for a review see Barnes & Bergström, 1988). Limited data is available from Baltica, which was situated close to 30°N of the tropics during the uppermost Ordovician (McKerrow &

Scotese, 1990, fig. 9; Figure 4.3). The fauna recovered from the uppermost Rawtheyan Jonstrop Formation of Sweden was dominated by *Amorphognathus ordovicicus* (28%), *Dapsilodus mutatus* (28%), *Panderodus sp.* (29%) and *Drepanoistodus suberectus* (8%; percentages calculated from sample 508; Bergström & Bergström, 1996). Other taxa that constituted 2% or less of the fauna included *Belodina confluens*, *Birksfeldia circumplicata*, *Protopanderodus liripipus*, *Pseudooneotodus beckmanni*, *Scabbardella altipes* and geniculate elements indet (Bergström & Bergström, 1996). This differs from all of the Sweet & Bergström (1984) biofacies and the biofacies discussed above from Laurentia. It lacks the genera commonly found within the Laurentian Shelf Biofacies and differs from the Shelf-edge Biofacies in being dominated by *Amorphognathus* and *Dapsilodus*. It may represent a previously undescribed biofacies.

In summary, in the uppermost Ordovician there is a marked difference in biofacies found on the shelf and those in shelf-edge and deeper-water sections. The genera within the Shelf Biofacies are similar to those recovered by Sweet & Bergström (1984) from shelf sections, but the sub-biofacies described by Sweet & Bergström (1984) can not be clearly observed. The Shelf-edge Biofacies differs in generally lacking *Amorphognathus*, but does contain a number of the coniform genera recovered by Sweet & Bergström (1984) from shelf-edge sections. There have been no reports of a Slope Biofacies dominated by *Dapsilodus mutatus* and *Periodon grandis* in the uppermost Ordovician.

4.2 Pattern of conodont extinction around Laurentia

4.2.1 Shelf Biofacies

4.2.1a Inner-shelf sections

Within the Oolitic Province of central Laurentia, the succession in Missouri comprises: the Maquoketa Shale (Upper Ordovician), the Noix Limestone (Hirnantian), Bowling Green Dolomite (early Silurian?), and Grassy Green Shale (Devonian) Formations all bounded by unconformities (McCracken & Barnes, 1982; Figure 4.5). In Oklahoma, the Sylvan Shale is unconformably overlain by the

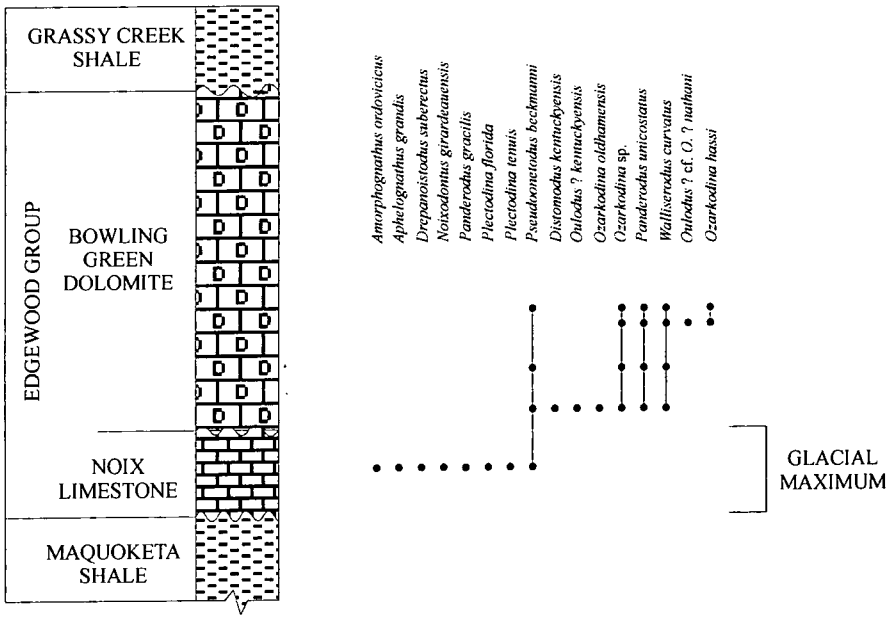


Figure 4.5 Conodont ranges through the Noix Limestone and Bowling Green Dolomite of Missouri. Drawn from abundance tables in McCracken & Barnes (1982).

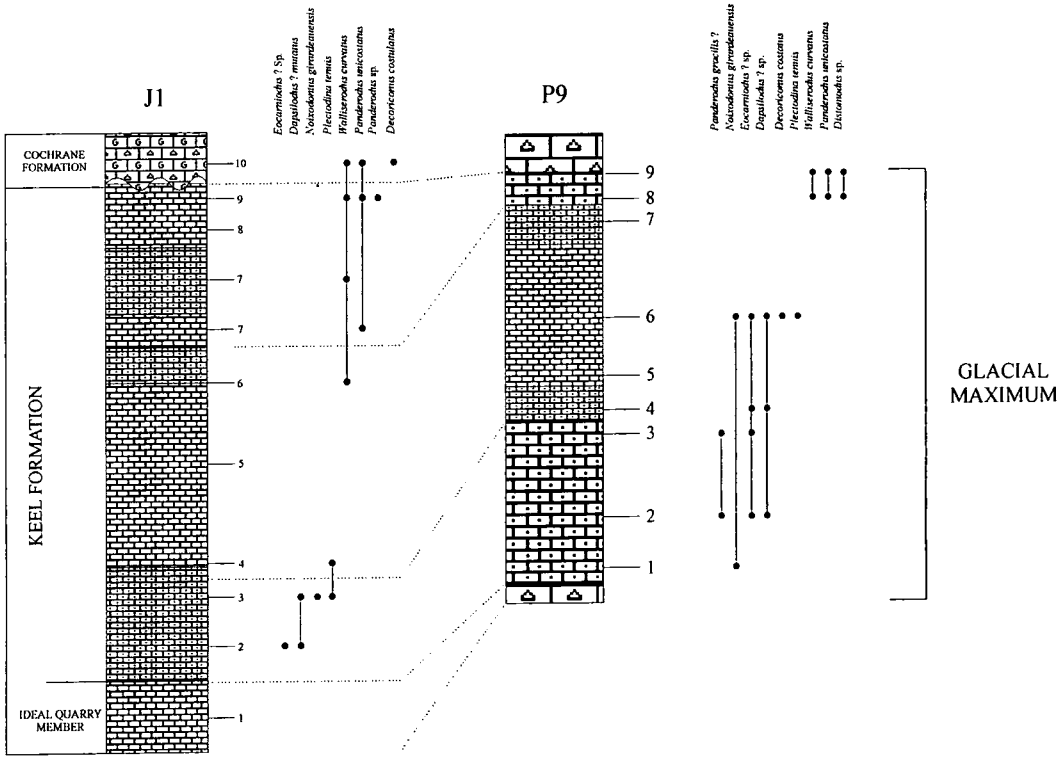


Figure 4.6 Conodont ranges through the Keel and Cochrane Formations of Oklahoma. Drawn from abundance tables in Amsden & Barrick (1986).

Hirnantian Keel Formation, which in turn is unconformably overlain by the Lower Silurian Cochrane Formation (Amsden & Barrick, 1986; Figure 4.6).

The glacial maximum is regarded as occurring within the Keel and Noix Limestone Formations (Oklahoma and Missouri), which can be correlated with Global Cycle H1 (Section 2.4.1). Here a basal oolitic limestone, bearing the *Hirnantia* Fauna, is overlain by laminated limestone (Amsden & Barrick, 1986). The basal oolitic sediments yield a diverse conodont fauna (*Noixodontus* Fauna) including *Noixodontus girardeauensis*, *Plectodina* sp., *Panderodus gracilis* and *Pseudooneotodus beckmanni.* Additionally, *Dapsilodus*? *mutatus*, *Decoriconus costulatus* and *Eocarniodus*? sp. were reported from Oklahoma (Amsden & Barrick, 1986), whereas *Amorphognathus ordovicicus* and *Drepanoistodus suberectus* were recovered in Missouri (McCracken & Barnes, 1982).

The elements of the *Noixodontus* Fauna in Oklahoma continued through the upper part of the Keel Formation, but became extinct prior to the formation of the unconformity at the base of the overlying Silurian strata (Amsden & Barrick, 1986). Consequently, Ordovician taxa became extinct within the glacial maximum, apart from the simple cone *Decoriconus costulatus*, which survived into the Silurian strata.

In the Missouri section, the *Noixodontus* Fauna was not recovered from strata above the oolitic Noix Limestone apart from *Pseudooneotodus beckmanni* (McCracken & Barnes, 1982). The overlying Bowling Green Dolomite yielded exclusively Silurian-type taxa (McCracken & Barnes, 1982). Thus, all elements of the fauna became extinct within the glacial-maximum interval, apart from *Pseudooneotodus beckmanni,* which ranged into the Silurian. Strata equivalent to the upper part of the Keel Formation of Missouri may be missing from this section, and McCracken & Barnes (1982) noted an unconformity between the Noix Limestone and the overlying Bowling Green Dolomite. Amsden & Barrick (1986) have since argued that the boundary between the Noix Limestone and the Bowling Green Dolomite is gradational and not a hiatus.

In Greenland, an Upper Ordovician fauna occurs in the mid-Turesø Formation and is dominated by taxa interpreted as shallow-water specialists (Armstrong, 1990). These

include *Rhipidognathus symmetricus,* known to have been associated with evaporitic facies elsewhere (Armstrong, 1990). These species do not range into the upper part of the Turesø Formation, which has yielded elements of *Panderodus unicostatus* prior to the appearance of *Ozarkodina hassi* (a Silurian-type taxa; Armstrong, 1990). This pattern of a significant gap in the conodont record, which yields only *Panderodus* elements, appears typical of the majority of inner-shelf sections in Greenland (Armstrong, 1990). The lack of well-constrained biostratigraphy (e.g. graptolite biozones, *Hirnantia* Fauna), geochemical studies and sea-level studies in the Greenland sections makes identification of the glacial maximum currently impossible. The significance of the gap in the conodont record is unknown.

In summary, inner-shelf settings sediments deposited during the glacial maximum contain a diverse fauna. Thus, the initiation of the glacial maximum may not have had a great effect on the conodont fauna. However, all elements of the fauna became extinct within the glacial maximum interval, apart from a few coniform taxa, which ranged into the Silurian.

4.2.1b Mid- to outer-shelf sections

The onset of the glacial maximum on Anticosti Island (Québec) can be located precisely by a positive $\delta^{13}C$ excursion that occurs within the Laframboise Member of the Ellis Bay Formation (see Underwood *et al.,* 1997; Figure 4.9). The Laframboise Member is underlain by the Lousy Cove Member, which is composed of sub-tidal carbonates (Long, 1993). The

Laframboise Member comprises a basal Oncolite Platform Bed (O.P.B.) overlain by a succession of bioherms and inter-bioherm sediments (Bioherm Unit), and is overlain by the transgressive Becscie Formation. Conodont ranges through the upper Ellis Bay Formation and lower Becscie Formation have been determined herein from sections on the western side of the island at Point Laframboise (Figure 4.7), Cap à l' Aigle and Lac Wickenden (Figure 4.8). Additional conodont information is provided by the studies of McCracken & Barnes (1981), Nowlan (1982) and Barnes (1988; Figures 4.9 & 4.10).

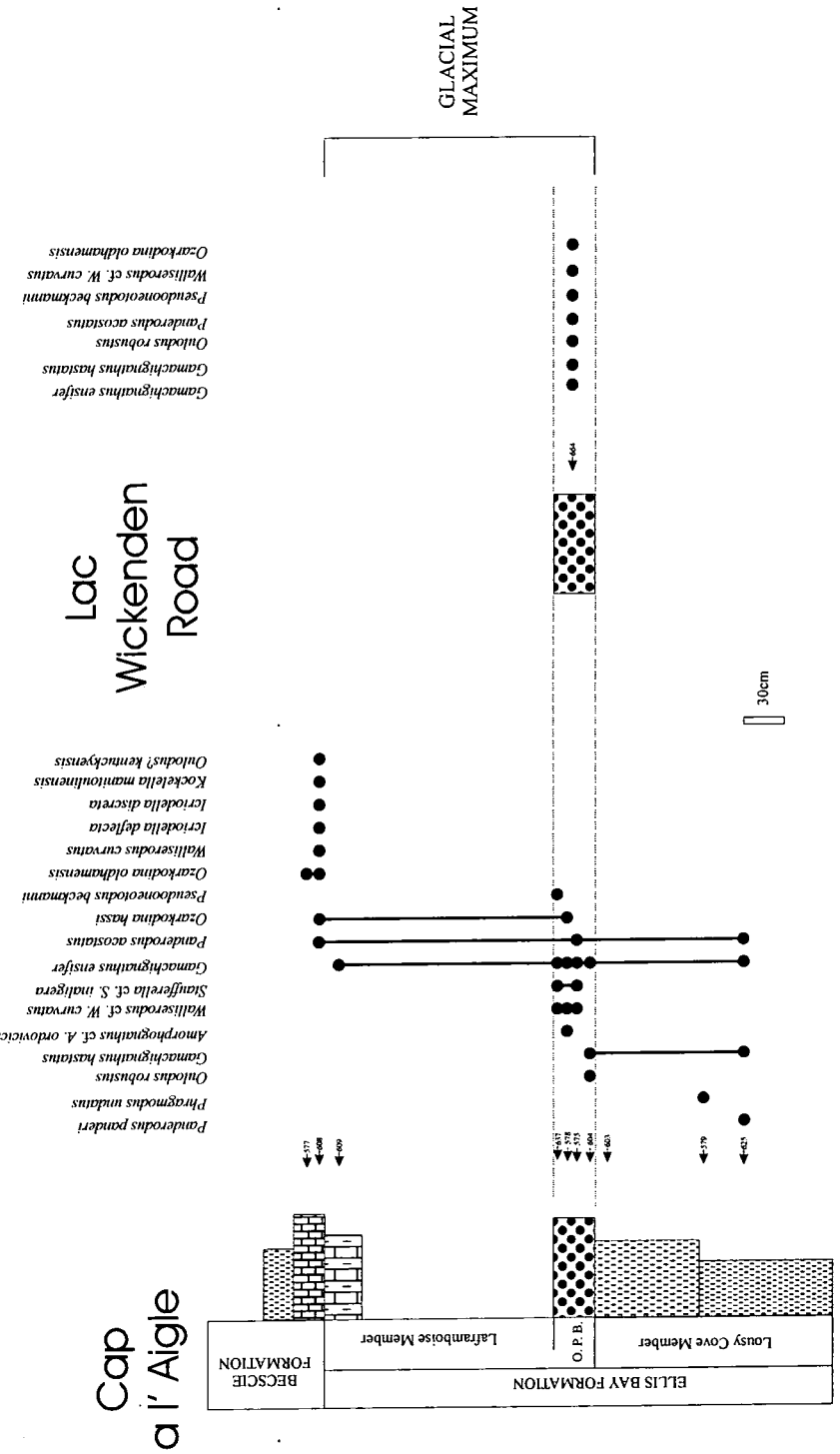


Figure 4.7 Conodont ranges through the Cap à l' Aigle section (Locality AI 2) and the Lac Wickenden Road grab sample (Stop AI 17a).

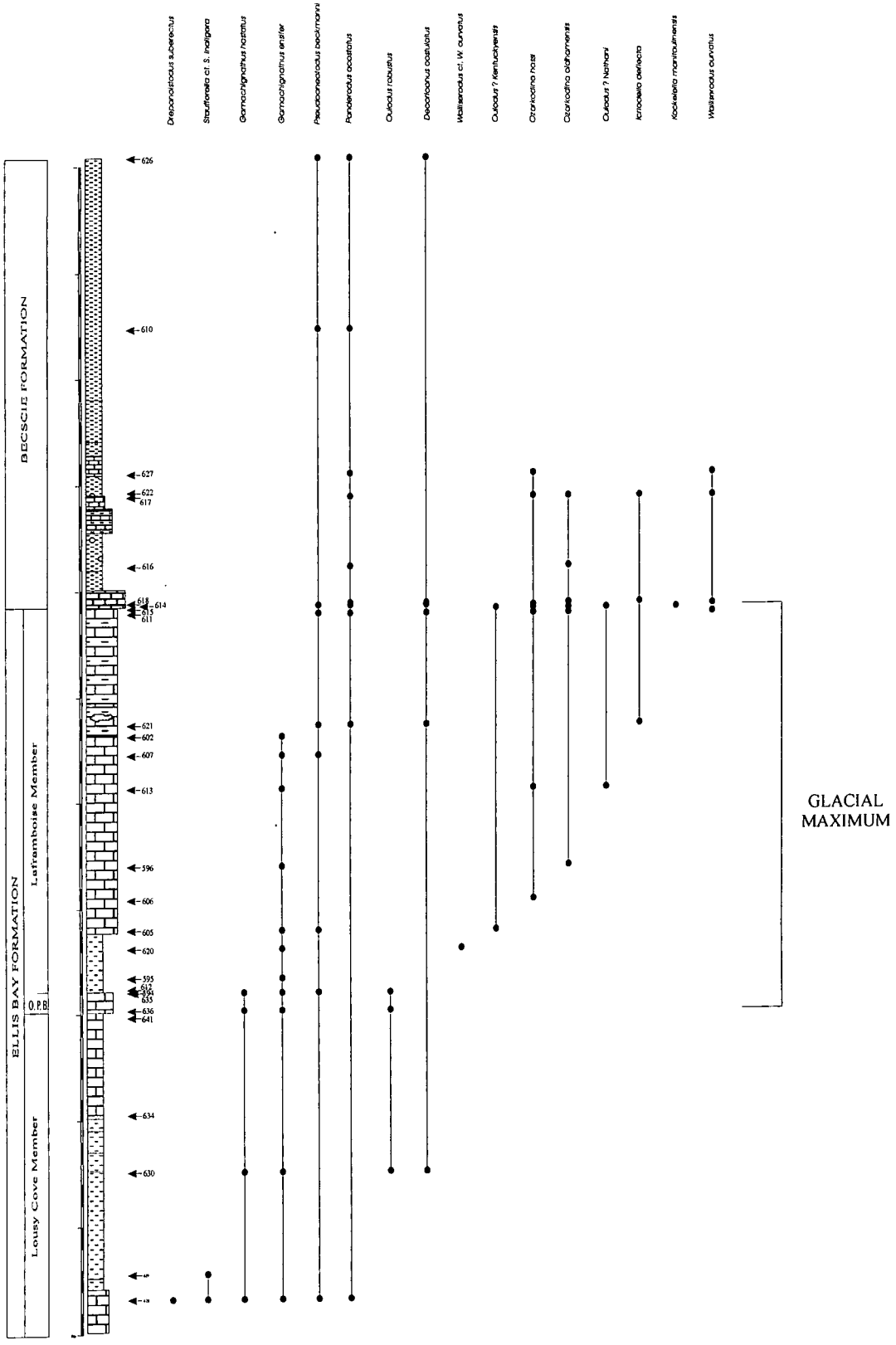


Figure 4.8 Conodont ranges through the Point Laframboise section (Locality AI 1). Each scale bar represents 20cm.

The Lousy Cove Member has yielded conodonts in sections from the western side of the island, including *Decoriconus costulatus, Gamachignathus ensifer, Gamachignathus hastatus, Oulodus robustus, Panderodus acostatus* (with serrate arcuatiform elements in sample AI 625), *Panderodus panderi, Phragmodus undatus, Pseudooneotodus beckmanni* and *Staufferella inaligera.* A more diverse fauna was recovered from the section at Salmon River (eastern side of the island) studied by McCracken & Barnes (1981), which may reflect a slightly deeper-water environment (see Sami & Deroches 1992).

All of the taxa within the Lousy Cove Member range up into the Laframboise Member apart from *Pseudobelodina dispansa, Pseudobelodina vulgaris, Panderodus liratus* and *Plegagnathus dartoni* (Barnes, 1988; Figure 4.9). Stepwise extinction of Ordovician species continued within the Laframboise Member and the basal beds of the Becscie Formation. *Aphelognathus* aff. *A. grandis, Oulodus ulrichi, Panderodus clinatus, Panderodus* cf. *P. staufferi* and *Plegagnathus nelsoni* have not been recorded from strata above the O.P.B. (herein; McCracken & Barnes, 1981; Barnes, 1988). *Amorphognathus ordovicicus, Gamachignathus hastatus, Oulodus robustus, Panderodus gibber* and *Walliserodus* cf. *W. curvatus* have not been recorded from above the Bioherm Unit (herein; McCracken & Barnes, 1981; Barnes, 1988). *Drepanoistodus suberectus, Gamachignathus ensifer, Oulodus rohneri, Phragmodus undatus, Pseudooneotodus mitratus* and *Staufferella inaligera* have not been recorded from the basal beds of the Becscie Formation (McCracken & Barnes, 1981; Barnes, 1988).

The first appearance of Silurian-type taxa is also stepwise. The first appearance of *Ozarkodina* occurred within the O.P.B. in the Cap à l' Aigle section and in the sample from Lac Wickenden Road (Figure 4.8). *Distomodus aff. D. kentuckyensis, Icriodella discreta, Kockelella manitoulinensis, Oulodus? kentuckyensis, Oulodus? nathani* and *Walliserodus curvatus* first appear within the Bioherm Unit and continue into the Silurian (herein, McCracken & Barnes, 1981, Barnes, 1988).

The final extinction of Ordovician-type species occurred within the basal Becscie Formation and was coincidental with a major transgression and the return to pre-glacial maximum isotope values (Underwood *et al.,* 1997; Section 3.3.3a). The only

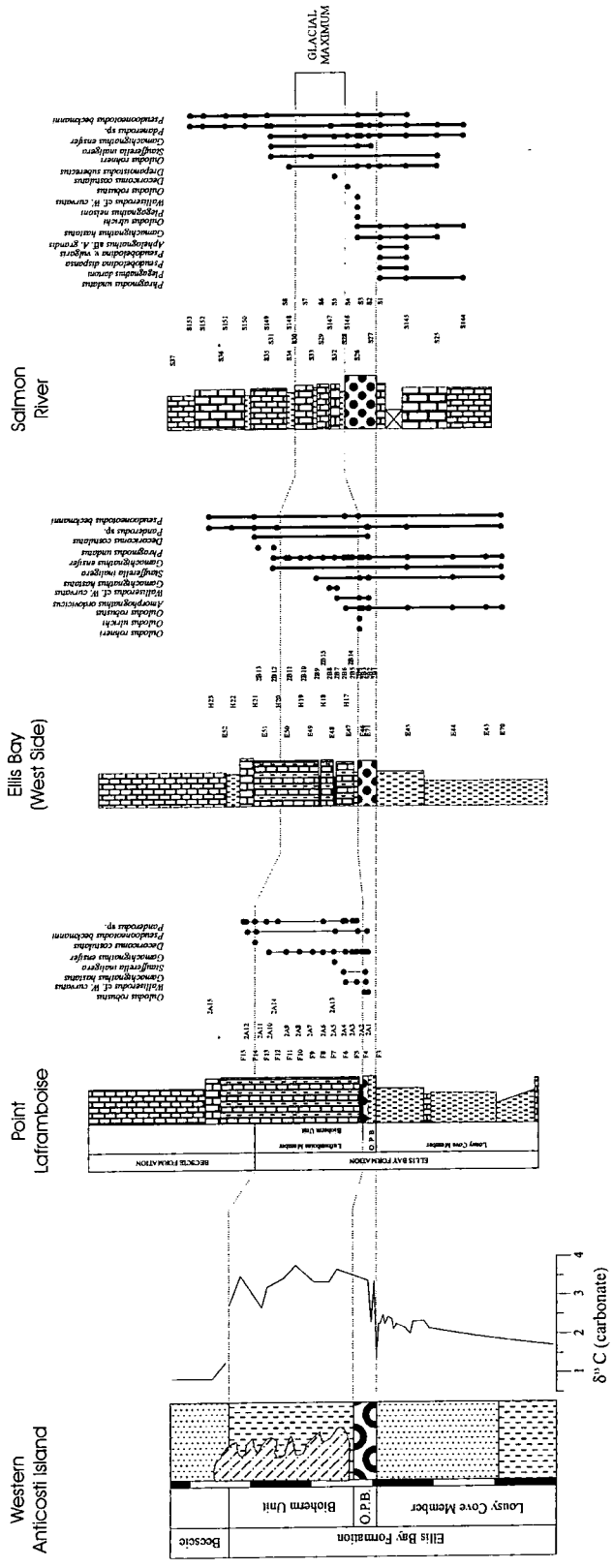


Figure 4.9 The stepwise extinction of conodont species through the upper Ellis Bay and Becscie Formations on Anticosti Island drawn from abundance tables in McCracken & Barnes (1981) and Barnes (1988). The onset of the glacial maximum is located by a positive $\delta^{13}C$ excursion, after Underwood *et al.*, (1997).

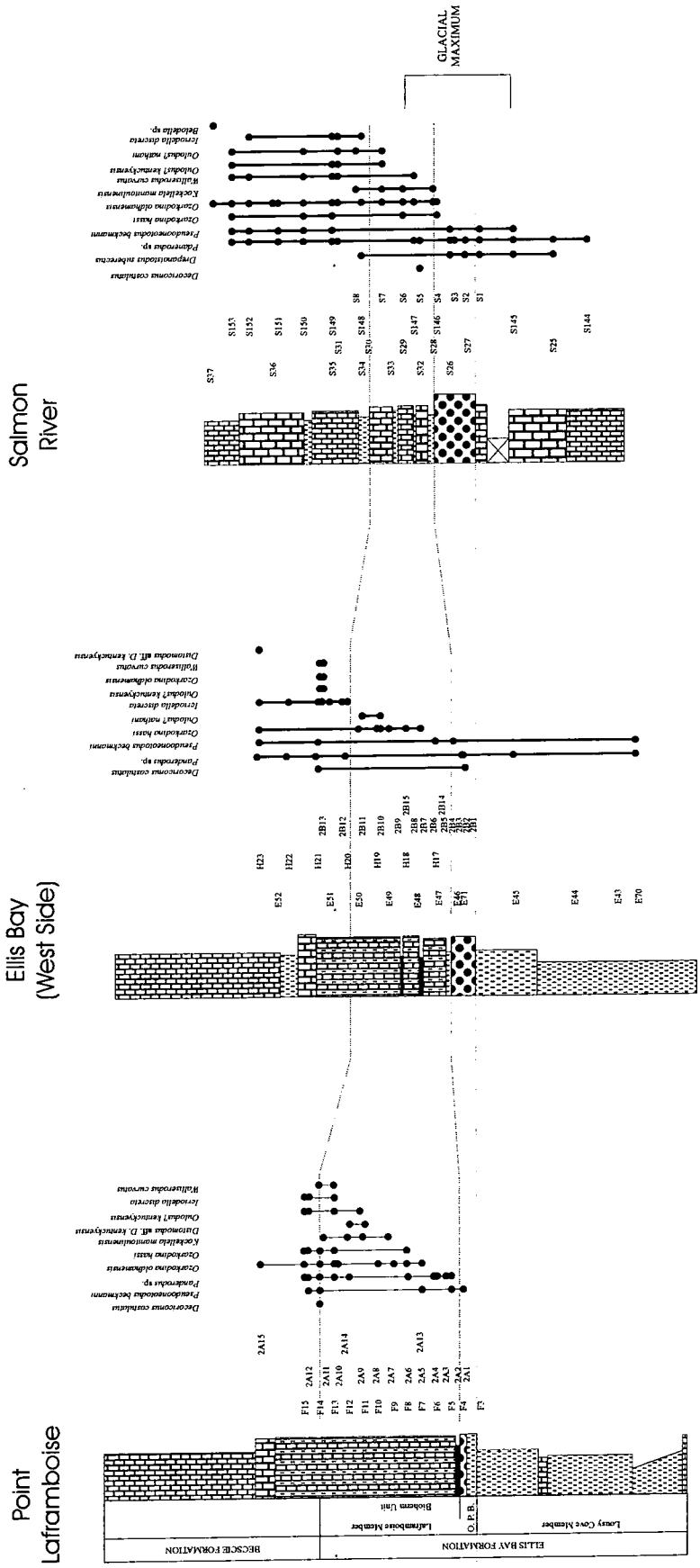


Figure 4.10 The stepwise appearance of Silurian-type conodont species through the upper Ellis Bay and Becscie Formations on Anticosti Island drawn from abundance tables in McCracken & Barnes (1981) and Barnes (1988).

species that were present within the Ordovician and continued above the basal Becscie Formation were *Decoriconus costulatus, Panderodus acostatus* and *Pseudooneotodus beckmanni* (Barnes, 1988). The fauna was not severely affected by the initiation of the glacial maximum. Extinctions occurred within the glacial maximum and the majority of species became extinct prior to the onset of the post-glacial transgression.

In the Percé area (Québec), the Upper Ordovician Burmingham Member of the White Head Formation yielded a diverse fauna including species of *Amorphognathus, Aphelognathus, Belodina, Oulodus, Drepanoistodus, Gamachignathus, Panderodus, Paraoistodus?, Phragmodus, Pseudooneotodus* and *Staufferella?* (Nowlan, 1981; Figure 4.11). The overlying Côte de la Surprise Member of the Whitehead Formation is of Hirnantian age (Lespérance *et al.*, 1981), and may be equivalent to the glacial maximum. Upper Ordovician conodonts became extinct, except for *Panderodus gibber* and *Panderodus gracilis*, directly below the Côte de la Surprise Member, which has not yielded conodonts (Nowlan, 1981; Lespérance *et al.*, 1981). Therefore, the extinction can be related to the onset of the glacial maximum.

In summary, the Shelf Biofacies was not severely affected by the initiation of the glacial maximum. Extinctions occurred through the glacial maximum and most species became extinct prior to the onset of the post-glacial transgression. However, in the Percé section (Québec) all elements of the fauna became extinct immediately prior to the glacial maximum (Nowlan, 1981). In this section basal Silurian sediments are also barren perhaps indicating severe local conditions.

4.2.2 Shelf-edge Biofacies in outer shelf and slope sections

The succession at Prongs Creek (northern Yukon) consists of Upper Ordovician platformal limestones (Platformal Limestone Unit) and a transitional limestone (Transitional Limestone Unit) of the Whittaker Formation, overlain by shales of the Road River Group (McCracken, 1989). The lack of detailed sedimentary and lithological data means that the glacial maximum can only be placed imprecisely within the upper part of the platformal limestone, which represents the shallowest-water deposits.

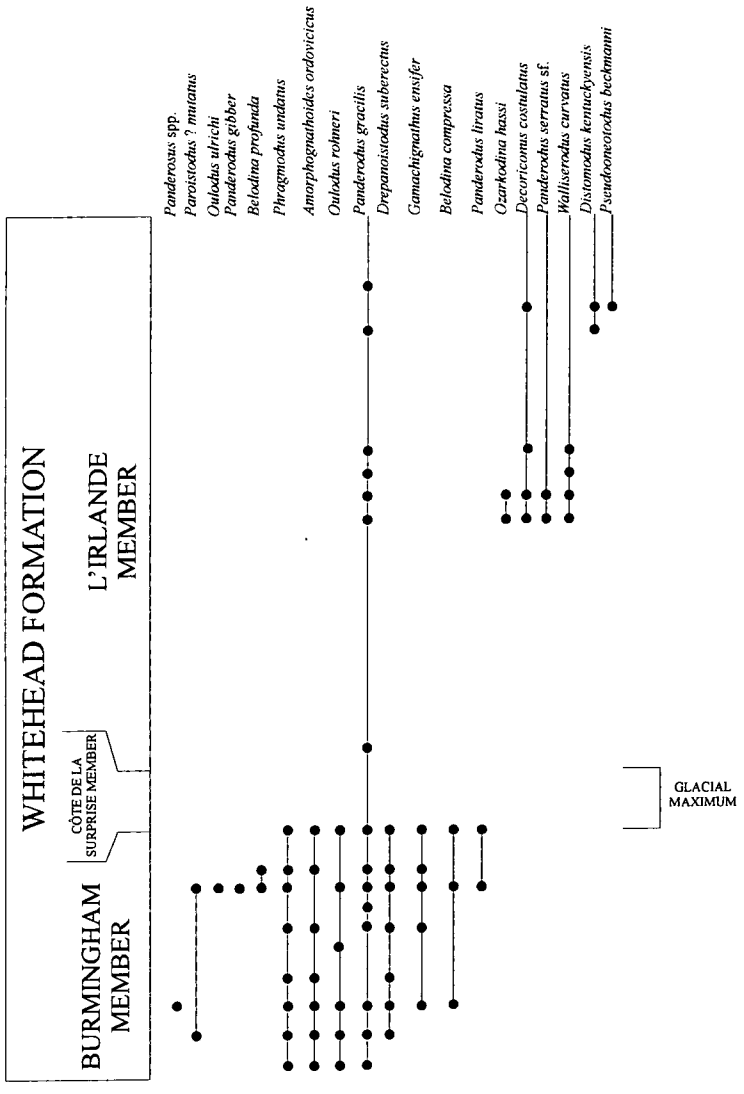


Figure 4.11 The extinction of conodont taxa within the Whitehead Formation, after Nowlan (1981). Nowlan (1981) did not include a lithological column.

The platformal limestones yielded only *Panderodus* elements and one element of *Belodina* sp. (McCracken, 1989; herein). A more diverse fauna including *Aphelognathus*, *Juanognathus*, and *Pseudobelodina* occurred lower in the section, but became locally extinct / disappeared within strata whose age can only be broadly estimated as mid - Maysvillian to Richmondian (McCracken, 1989).

The uppermost Ordovician platformal limestones are overlain by a transgressive, transitional limestone, which yields a diverse conodont fauna of Silurian aspect. The fauna includes *Dapsilodus obliquicostatus, Decoriconus costulatus*, *Distomodus* cf. *D. kentuckyensis, Oulodus* cf. *O. panuarensis, Pseudolonchodina expansa, Walliserodus curvatus*, Gen. sp. Indet A. and species of *Panderodus*. A similar pattern of extinction is seen in the adjacent shelf-edge section at Royal Creek (McCracken, 1989). Extinction occurred prior to the end-Ordovician fluctuations in climate and may be due to local environmental conditions.

In the Avalanche Lake section (Mackenzie Mountains), a succession of Beds D-A (A being the youngest) of the Whittaker Formation span the extinction interval. The glacial maximum occurs within Bed C, the point of maximum regression, and coincides with a positive $\delta^{13}C$ isotope excursion (Nowlan *et al.*, 1988; Wang *et al.*, 1993). Bed D and C contain a diverse end-Ordovician fauna mainly indicative of the Midcontinent province, including *Besselodus, Coelocerodontus, Decoriconus, Drepanoistodus, Oulodus, Panderodus, Paraoistodus*, *Plectodina, Protopanderodus, Pseudobelodina, Pseudooneotodus, Staufferella, Walliserodus* and *Zanclodus* (Nowlan *et al.*, 1988: Figure 4.12).

Only *Decoriconus costulatus* and *Panderodus gracilis* have been recovered from strata above the middle part of Bed C (Nowlan *et al.*, 1988). Bed B represents the basal part of the post-glacial transgression and has only yielded elements of *Panderodus gracilis* and *Walliserodus curvatus* (Nowlan *et al.*, 1988). Continued transgression in Bed A saw the first appearance of the Silurian-type taxa *Dapsilodus*? sp. A and *Ozarkodina hassi* (Nowlan *et al.*, 1988). Therefore, extinction of the Ordovician species occurred within Bed C prior to the post-glacial transgression, within the glacial maximum.

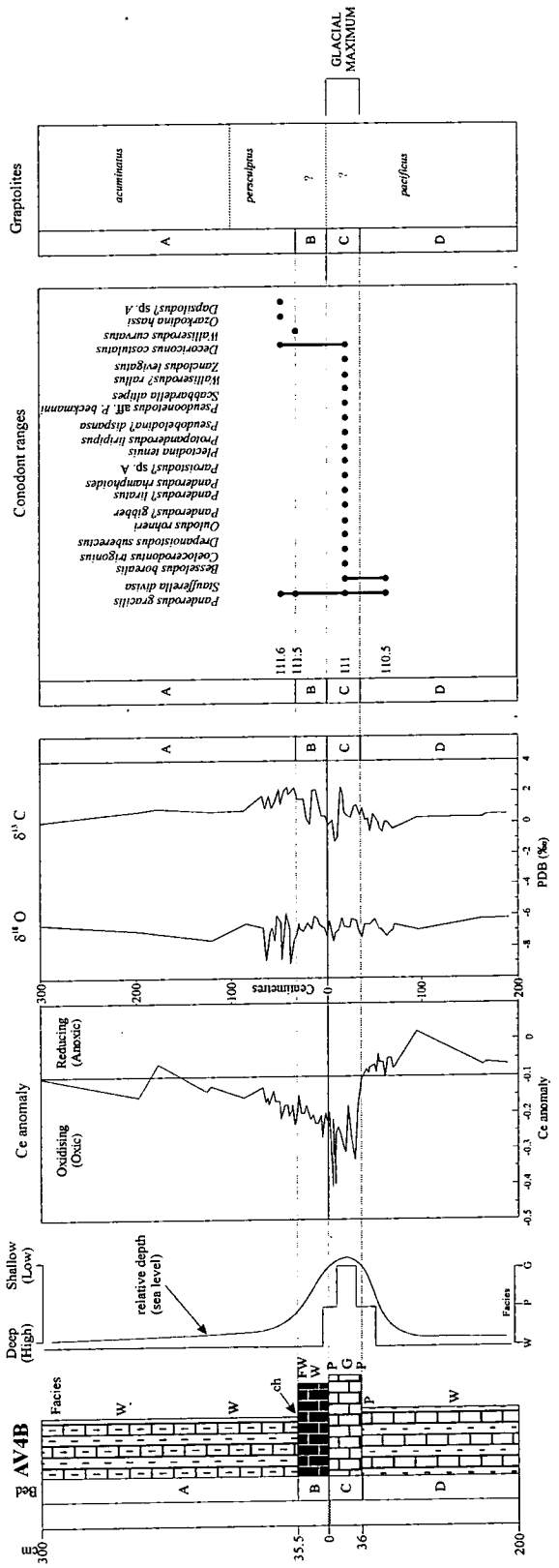


Figure 4.12 Conodont extinction within the Avalanche Lake section compared with lithological, sea level and geochemical data. After Wang *et al.* (1993b). The conodont data is from Nowlan *et al.* (1988). Refer to Figure 2.22 for the microfacies key.

Within the Cornwallis Island section (Canadian Arctic), the *pacificus* to *acuminatus* GBZs have been sampled for conodonts within the Cape Phillips Formation by Melchin *et al.* (1991). Here, the glacial maximum occurs within the '*bohemicus* GBZ', and is represented by a glauconitic siltstone, interpreted as the shallowest bed in the section (Melchin *et al.*, 1991). The relationship between the '*bohemicus*' and *extraordinarius* GBZs has been debated in Chapter 2 (Section 2.3.1).

Within the *pacificus* GBZ, the diverse Ordovician fauna was dominated by coniform species plus *Amorphognathus ordovicicus* and *Plectodina* sp. Species that are not seen above the *pacificus* GBZ include *Belodina confluens*, *Besselodus sp.*, *Coelocerodontus trigonius*, *Panderodus feulneri*, *Plectodina* sp., *Plegagnathus nelsoni*, *Protopanderodus insculptus*, *Pseudobelodina vulgaris*, *Pseudooneotodus mitratus*, *Scabbardella altipes* and *Walliserodus amplissimus* (Melchin *et al.*, 1991). The overlying '*bohemicus* GBZ' yielded only a small number of *Drepanoistodus suberectus* and *Panderodus* sp. elements (Melchin *et al.*, 1991). Within the transgressive shales of the *persculptus* GBZ, *Amorphognathus ordovicicus* and a number of coniform taxa reappeared (*Drepanoistodus suberectus*, *Panderodus gracilis*, *Paraoistodus*? sp. A, *Pseudobelodina*? *dispansa* and *Pseudooneotodus beckmanni*). The first appearance of Silurian-type taxa (*Oulodus*? *kentuckyensis*) also occurred within the *persculptus* GBZ (Melchin *et al.*, 1991). A second phase of extinction occurred within the *acuminatus* GBZ, *Amorphognathus*, *Paraoistodus*? and *Pseudobelodina*? disappeared. *Decoriconus costulatus* and *Panderodus gracilis* were the only survivors of both events. Thus, extinction occurred at the onset and cessation of the glacial maximum within the Cornwallis Island succession.

The survival of *Scabbardella* into the *persculptus* GBZ occurred within the trough sections of the Selwyn Basin. Upper Ordovician limestones yielded a fauna dominated by coniform genera, *Amorphognathus* and rare representatives of the Midcontinent Faunal Province (Lenz & McCracken, 1982). At Pat Lake South, *Scabbardella* survived into the *persculptus* GBZ, whilst the rest of the Ordovician fauna disappeared (Lenz & McCracken, 1982). In summary, extinctions occurred within the Shelf-edge Biofacies in the upper *pacificus* GBZ. *Amorphognathus*, *Scabbardella* and *Paraoistodus* ranged higher, but also eventually succumbed to extinction in the *acuminatus* GBZ during the post-glacial transgression.

Within the basinal Dob's Linn section, conodonts on bedding planes within shales of the *pacificus* to *acuminatus* GBZs have been studied by Barnes & Williams (1988). The glacial maximum has been interpreted as occurring within the upper *pacificus* to upper *extraordinarius* GBZs by Armstrong & Coe (1997) based on sedimentological evidence. A positive $\delta^{13}C$ excursion has also been identified within the *extraordinarius* GBZ by Underwood *et al.* (1997).

The *anceps* (= *pacificus*) GBZ yielded a low-diversity fauna including *Amorphognathus*, *Protopanderodus*, *Scabbardella* and *Hamarodus* (Barnes & Williams, 1988). *Hamarodus* and *Protopanderodus* do not range above this biozone and no conodonts were recovered from the *extraordinarius* GBZ. Within the *persculptus* GBZ, *Amorphognathus* and *Scabbardella* reappeared, and were joined by the Silurian species *Dapsilodus obliquicostatus*. *Amorphognathus* and *Scabbardella* became extinct within the *persculptus* GBZ. Shales of the *acuminatus* GBZ yielded only two rare coniform taxa, *Dapsilodus* and *Decoriconus* and an element referred to *Oulodus*?. Therefore, the pattern of extinction in the Dob's Linn section is similar to that described above in the Shelf-edge Biofacies. Extinctions occurred in the upper *pacificus* GBZ possibly associated with the onset of the glacial maximum. *Amorphognathus* and *Scabbardella* survived into the *persculptus* GBZ, but have not been recorded in the *acuminatus* GBZ.

4.2.3 Summary of pattern on Laurentia

The present evidence suggests that in the inner- to outer-shelf sections, conodont species were not severely affected by the initiation of the glacial maximum (Figure 4.13). An exception is the section at Percé (Québec) where all elements of the fauna became extinct immediately prior to the glacial maximum (Nowlan, 1981). In general, extinctions within the Shelf Biofacies occurred through the glacial maximum with most species becoming extinct prior to the onset of the post-glacial transgression. However, some survivors have been identified in the Anticosti Island section (Québec) within the initial post-glacial transgression.

Extinction of species of the Shelf-edge Biofacies occurred in the upper *pacificus* GBZ, with species of *Amorphognathus*, *Scabbardella* and *Paraoistodus* occurring higher. However, these genera also succumbed to extinction in the *acuminatus* GBZ during the post-glacial transgression.

Upper Ordovician species that survived both phases of extinction unaltered and continued into the Silurian in all areas were exclusively coniform taxa (Barnes & Bergström, 1988). *Decoriconus costulatus, Pseudooneotodus beckmanni* and several species of *Panderodus* (*Panderodus gibber*, *Panderodus gracilis*, *Panderodus unicostatus*) were the only species to survive. A number of Silurian-type taxa (*Distomodus, Icriodella Oulodus*?, *Ozarkodina*) first appeared during the glacial maximum and survived into the Silurian. They may be termed Crisis Progenitor Taxa (Section 1.8) as they first appeared during a time of crisis. Their evolutionary significance will be discussed further in Chapter 5.

4.3 Pattern of conodont extinction on other Palaeo-continents

Although uppermost Ordovician and Silurian strata have been identified on other palaeocontinents few sections have been sampled for conodonts (for a review see Barnes & Bergström, 1988). Limited data is available from Baltica, which was situated close to 30°N of the tropics during the uppermost Ordovician (McKerrow & Scotese, 1990, fig. 9; Figure 4.3).

4.3.1 Baltica

In Sweden the succession comprises the Jonstrop (Rawtheyan), Loka (Hirnantian) and Motala (Rhuddanian to Aeronian) Formations (Bergström & Bergström, 1996). The Loka Formation (previously the *Dalmanitina* Beds) is characterised by shallow-water Hirnantian sediments (Bergström & Bergström, 1996) within which the glacial maximum can be tentatively placed.

The upper beds of the Jonstrop Formation yielded a fauna indicative of the Atlantic Faunal Region, which included *Amorphognathus ordovicicus*, *Belodina confluens*, *Birksfeldia circumplicata, Dapsilodus mutatus, Drepanoistodus suberectus,*

Panderodus sp., *Protopanderodus liripipus*, *Pseudooneotodus beckmanni*, *Scabbardella altipes* and geniculate elements indet (Bergström & Bergström, 1996). *Belodina confluens* died out within the Jonstrop Formation, with the remaining fauna ranging into the Loka Formation, in which they were joined by Silurian-type taxa. The Ordovician-type taxa became extinct within the Loka Formation, apart from *Panderodus* sp. and *Pseudooneotodus beckmanni*, which ranged into the Silurian Motala Formation.

The pattern of extinction in this section is similar to that seen in shelf settings in Laurentia. Only minor extinction occurred prior to the Hirnantian, with most elements of the Ordovician fauna succumbing to extinction within the glacial maximum.

4.4 Discussion

4.4.1 Timing of extinction events

It has been discussed in Section 4.1 that two studies of the timing of the Upper Ordovician conodont extinction events differed in their conclusions (Figure 4.1). The Melchin *et al.* (1991) study showed that two phases of extinction occurred, within the upper *pacificus* GBZ (start of the glacial maximum), and within the *acuminatus* GBZ (post-glacial transgression). Alternatively, Armstrong (1995) concluded that a major conodont extinction event occurred in the upper '*bohemicus* GBZ' (end of the glacial maximum), with a minor event occurring within the lower *acuminatus* GBZ (post-glacial transgression). Armstrong's (1995) conclusion was mainly based on shallow-water sections and thus, identifies the pattern outlined herein seen within the Shelf Biofacies. The Melchin *et al.* (1991) study was based on the outer-shelf section at Cornwallis Island and so the conclusions of that study compare favourably with the pattern observed in the Shelf-edge Biofacies herein.

4.4.2 Cause of extinction events

The onset of the glacial maximum (first strike) severely affected cooler, deeper-water conodont faunas. Extinctions have been attributed to lowering of sea-water

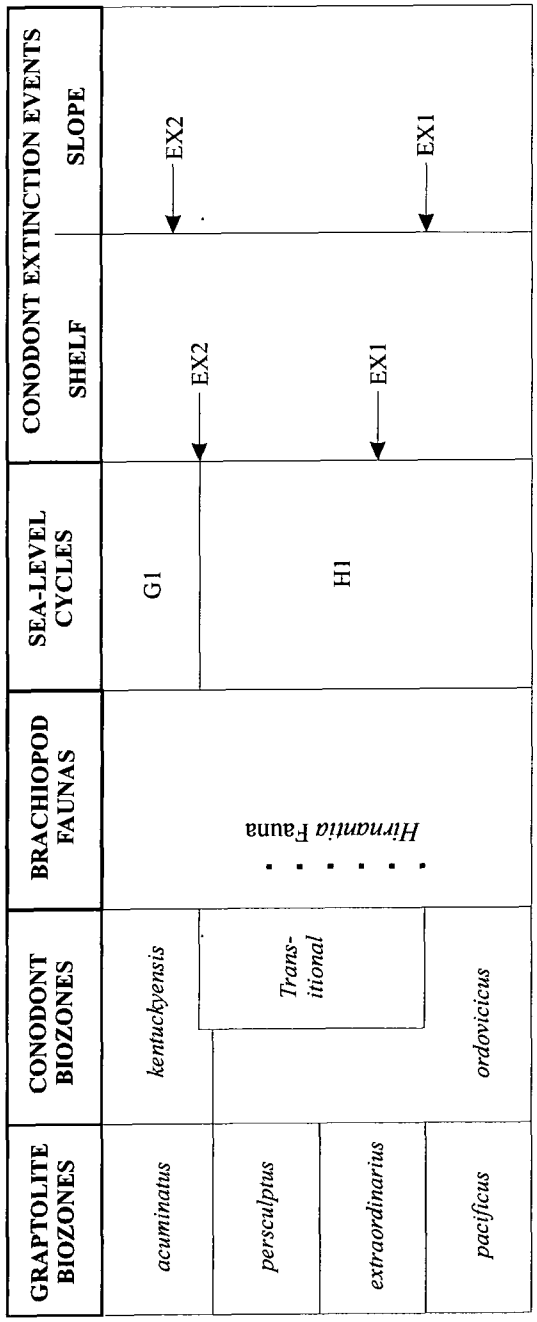


Figure 4.13 A summary of the timing of conodont extinction events across the Ordovician–Silurian boundary.

temperature (a decrease of ~8°C), the movement of climatic belts and sea-level fall (Brenchley *et al.,* 1995). Brenchley *et al.* (1995) suggested rapid changes in ocean circulation as the primary cause in the first strike of extinction. The preferential extinction of deep-water conodont taxa does suggest ocean cooling and the introduction of cold-water currents was the likely causal mechanism.

Conodont faunas that inhabited shallow-water settings were less affected by the onset of the glacial maximum, but suffered extinction within the glacial maximum. Brenchley *et al.* (1995) suggested that oceanic cooling intensified within the Hirnantian and extinctions on the shelf may have resulted from the increasing intensity of cooling and renewed shallowing (e.g. Brenchley *et al.,* 1995). Other possible causes of extinction of the Shelf Biofacies include overcrowding, as the regression and rising permanent thermocline forced faunas into the mid- to outer-shelf settings (Sheehan, 1988).

A number of conodont species in deeper-water settings survived the glacial maximum (e.g. *Amorphognathus*), but became extinct during the post-glacial transgression. The extinctions may have resulted from increasing water temperatures, rising anoxia and the cessation of oceanic circulation (Brenchley *et al.* 1995; Goodfellow *et al.*, 1992).

4.5 Conclusions

- A Shelf and Shelf-edge Biofacies can be identified in the uppermost Ordovician.
- A Slope Biofacies dominated by taxa such as *Dapsilodus* has not been identified in the uppermost Ordovician.
- The pattern of conodont extinctions varies in different palaeoenvironments.
- In shelf-edge and slope sections, conodonts suffered extinction within the upper *pacificus* to *extraordinarius* GBZs, associated with the onset of the glacial maximum, and during the post-glacial transgression.

- In inner- and mid-shelf sections conodonts were not severely affected by the initiation of the glacial maximum, but became extinct within the glacial maximum to post-glacial period.

- Extinctions were caused by the changes in sea-level temperature, habitat space and oceanic circulation associated with the initiation, intensification and cessation of the glacial maximum.

Chapter 5

Recovery of conodonts following the end-Ordovician mass extinction event.

Chapter 5

Recovery of conodonts following the end-Ordovician mass extinction event.

5.1 Introduction

The end-Ordovician extinction event terminated an episode of maximum conodont diversity (Sweet, 1985; Barnes & Bergström, 1988). It has been suggested that most of the long established stocks disappeared and were replaced by only a small number of new lineages (Sweet & Bergström, 1984). Species diversity declined gradually through the Ashgill followed by a short, intense interval of extinction in the latest Ashgill (Barnes & Bergström, 1988). Barnes & Bergström (1988) estimated that the initial recovery involved the replacement of 25 Ordovician-type genera, with 15 Silurian-type genera, including eight that survived the extinction event.

Research into the recovery of conodonts following the end-Ordovician mass extinction event has been almost exclusively limited to a number of isolated observations. For example, it has been suggested that the survivors were all Ecological Generalists, with simple morphologies, that re-occupied the seas immediately after transgression (McCracken & Barnes, 1982; Barnes & Bergström, 1988).

Two general, conflicting hypotheses exist regarding the identity of the Ordovician source of new taxa during the initial recovery interval: the slope (Atlantic Faunal Region) or shelf (Midcontinent Faunal Region). Sweet & Bergström (1974) suggested that the taxa characteristic of the Atlantic Faunal Region disappeared and that the ancestors of essentially all Silurian taxa originated in the Midcontinent Faunal Region (Sweet & Bergström, 1974; Bergström, 1990). The few Silurian taxa that descended from species of the Atlantic Faunal Region evolved from those species that had most frequently migrated into the Midcontinent Faunal Region (Sweet & Bergström,

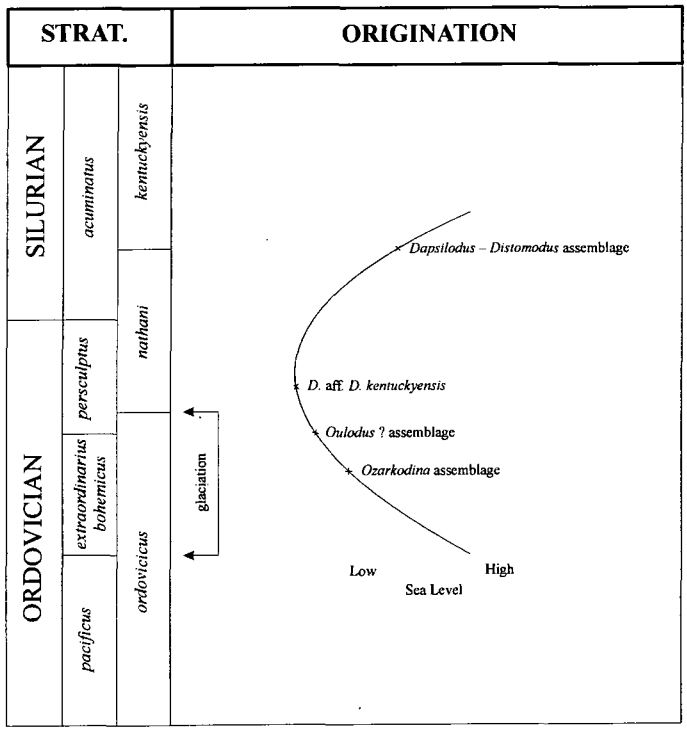


Figure 5.1 Conodont recovery events identified by Armstrong (1996) in the uppermost Ordovician and lowermost Silurian.

GRAPTOLITE BIOZONES	CONODONT BIOZONES	ALDRIDGE *et al.*(1993b)	HEREIN
	amorphognathoides	Ireviken Event	*amorphognathoides*
crenulata		Snipklint	
griestoniensis		Primo	
crispus	*celloni*		*celloni*
turriculatus		S-P Event	
			bullatus
sedgwickii	*staurognathoides*	Malmøykalven Secundo	Low Diversity
		Sandvika Event	*staurognathoides/ tenuis*
convolutus		Jong Primo	
leptotheca			
magnus			
triangulatus			
cyphus	*kentuckyensis*	Spirodden Secundo	*kentuckyensis*
acinaces			
atavus			
acuminatus			
persculptus		P-S Event	

Figure 5.2 Comparison of the conodont recovery episodes identified herein and the episodes and events identified by Aldridge *et al.* (1993b).

1974). Alternatively, Armstrong (1996), in the only study that has specifically examined the initial recovery of conodonts following the end-Ordovician extinction event, suggested that the initial recovery was fuelled by the phylogenetic emergence of taxa from the slope (bathyal ecozone) onto the shelf during the extinction event. He suggested that conodonts which had evolved in the bathyal ecozone during the Ashgill were forced into low latitude, shallow water by a rising thermocline during the end-Ordovician glaciation and after the glaciation were driven into shallow water by rising anoxia. He identified a number of recovery assemblages (*Ozarkodina*, *Oulodus*?, *Distomodus* aff. *D. kentuckyensis* and *Dapsilodus* - *Distomodus*) and outlined their stepwise appearance (Figure 5.1).

Little work has commenced on the testing of the Armstrong (1996) and Sweet & Bergström (1974) hypotheses against the fossil record. A number of other areas have also remained virtually unstudied:

- The pattern of initial and long-term recovery.
- The origins of Llandovery taxa.
- The mechanisms hindering and driving recovery.
- The applicability of the general recovery models.
- The effect of the extinction event and recovery on the composition and distribution of conodont biofacies.

Detailed study of the initial and long-term recovery of conodonts in sections around Laurentia has allowed the identification of a number of origination / extinction episodes through the uppermost Ordovician and Lower Silurian (Llandovery), which can be linked to variations in climate through the recovery interval. The pattern of recovery on Laurentia is tested against conodont data from other palaeocontinents and the current general models of biotic recovery. The distribution and composition of Llandovery conodont biofacies are compared with the well-documented, Upper Ordovician biofacies.

5.1.1 General Recovery models and terminology

A number of possible methods of speciation following an extinction event have been suggested. These include allopatric, parapatric and sympatric speciation. Speciation can occur when a population becomes totally (allopatric speciation) or partially geographically isolated (parapatric speciation; Charlesworth, 1990). An alternative method is genetic isolation, which can come about by preferential mating within a spatially heterogeneous population (sympatric speciation; Charlesworth, 1990). Differentiation between these three speciation mechanisms is difficult to ascertain from the fossil record.

The models and general terminology used in the study of recovery have been discussed in Chapter 1 (Sections 1.4 & 1.8). Two general models for initial recovery of faunas following an extinction event are documented in the literature; one suggesting that survivors would be limited to Ecological Generalists (Jablonski, 1986), and the other suggesting that a much more diverse rootstock would survive and enable rapid recovery (Harries *et al.*, 1996; Figure 1.2).

Kauffman & Harries (1996) outlined the range of potential survivors involved in recovery, and mechanisms enabling their survival (Figure 5.3). The two main groups of survivors were taxa that survived in their primary habitat and taxa that migrated to a secondary habitat (refugia) prior to, or during, the extinction event. Taxa that could survive in their primary habitat included Ecological Generalists not affected by the environmental changes resulting in the extinction event, and widely dispersed taxa that were greatly reduced during mass extinction, but survived in pockets (Stranded Populations). Specialists that could have survived within their primary habitats include taxa with adaptations which enabled their survival (Pre-Adapted Survivors), or taxa adapted to the environmental conditions that prevailed during the extinction event (Disaster Species, Ecological Opportunists and Crisis Progenitor Taxa).

Refugia are habitats protected from the environmental changes that would otherwise lead to extinction. Taxa that migrate into a refuge (Refugia Taxa) during or prior to an extinction event may rapidly return to their primary habitat unchanged following

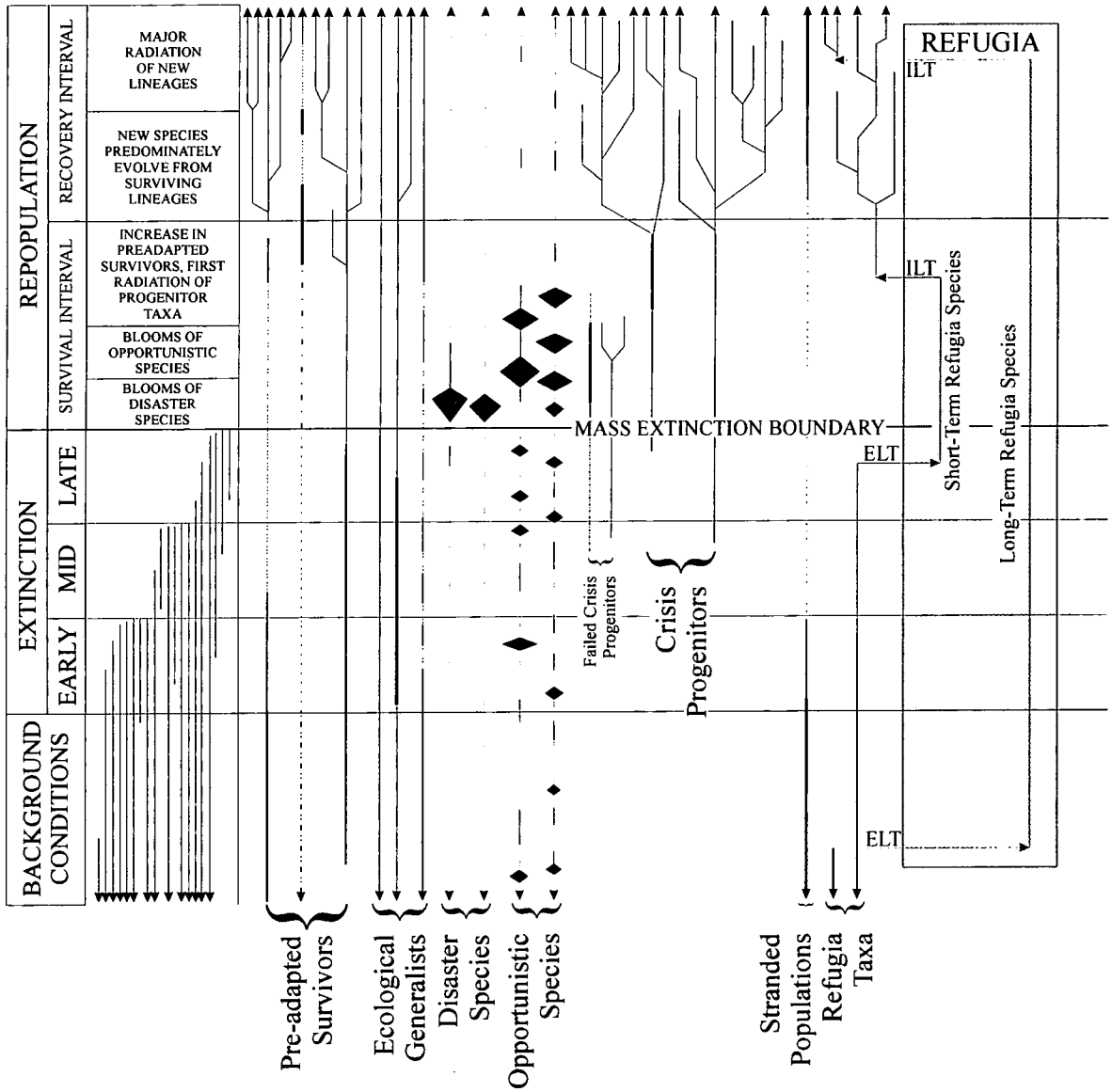


Figure 5.3 Model of survival and recovery from Kauffman & Harries (1996). For term definitions, refer to Section 1.8. ELT, Emigrant Lazarus Taxa; ILT, Immigrant Lazarus Taxa. The width of the solid lines depict the relative abundance of taxa and dotted lines represent intervals of non-occurrence. Arrows represent emigration or immigration of refugia taxa.

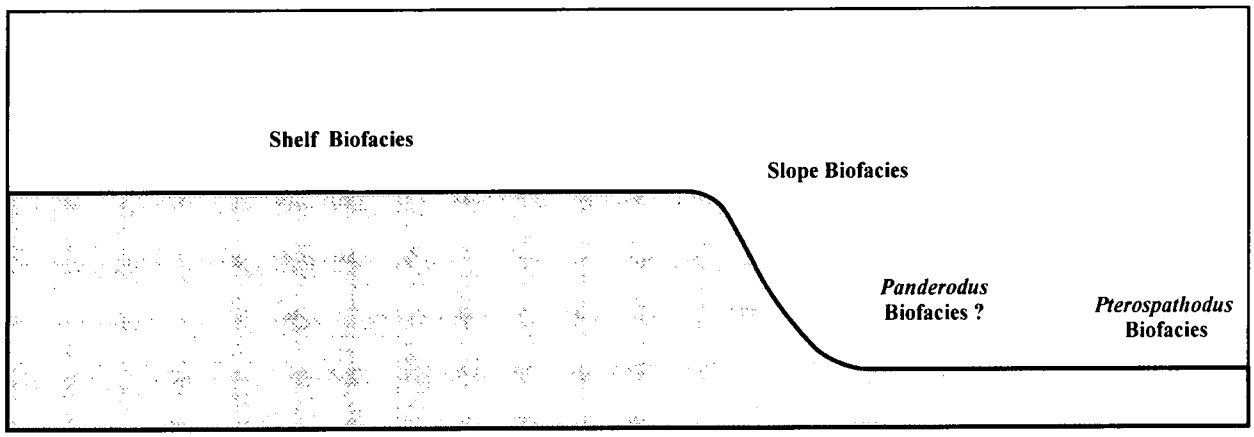
climate amelioration (Short-Term Refugia Taxa) or remain and evolve within the secondary habitat for a long period before returning (Long-Term Refugia Taxa). Kauffman & Harries (1996) suggested that Pre-Adapted Survivors, Short-Term Refugia Taxa and Crisis Progenitor Taxa were the main groups of taxa that could fuel rapid initial recovery. Pre-Adapted Survivors and Short-Term Refugia Taxa would be already adapted to specific habitats, which they would occupy following the extinction event. Thus, Crisis Progenitor Taxa have been suggested to be the main source of evolutionary innovation during or following an extinction event (Kauffman & Harries, 1996).

The Kauffman & Harries (1996) model is concerned with the initial pattern of recovery following an extinction event. Although a model specifically detailing long-term recovery has not yet been developed, the long-term recovery of species may be described in terms of macroevolutionary theories. If long-term recovery is consistent with the Punctuated Equilibrium Model of Gould & Eldredge (1993), it would occur as a series of rapid speciation events separated by periods of stasis. The *Plus ça change* Model of Sheldon (1996) predicts that punctuated equilibrium would occur in widely fluctuating physical environments, and that in less changeable environments, continuous gradualistic evolution would dominate. The pattern of conodont recovery through the Upper Ordovician and Lower Llandovery will be used to test the standard models discussed above.

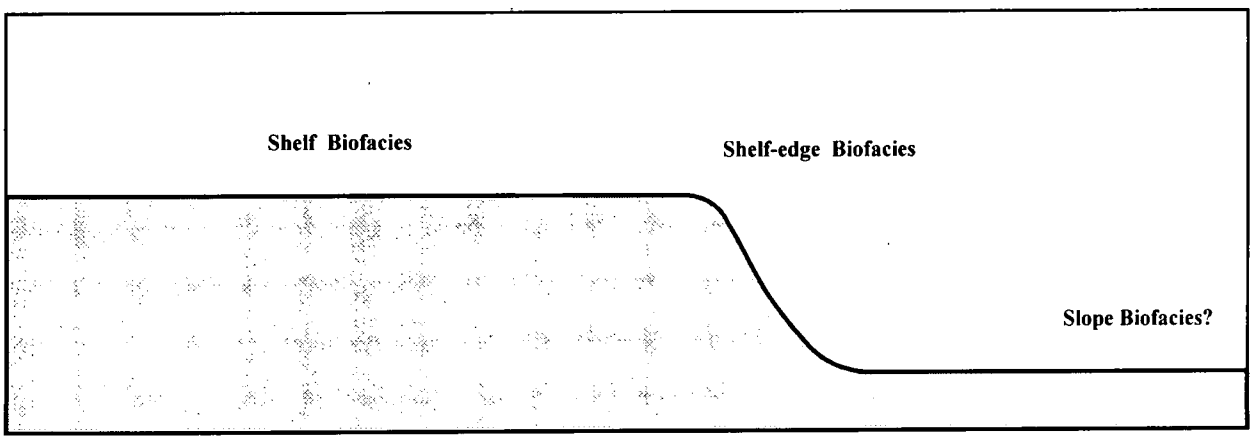
5.1.2 Llandovery Conodont Biofacies

The Shelf Biofacies and Slope Biofacies differentiated in the Upper Ordovician, can also be identified within the Llandovery (Armstrong, 1990; McCracken, 1991b; Watkins & Kuglitsch, 1997; Figure 5.4). The Lower Llandovery Shelf Biofacies was dominated by *Panderodus,* in association with *Distomodus*, *Icriodella*, *Kockelella*, *Oulodus* and *Ozarkodina* (Armstrong, 1990; Watkins & Kuglitsch, 1997). For example, a sample recovered from a shelf section in the Michigan Basin by Watkins & Kuglitsch (1997) comprised species of *Panderodus* (49%), *Ozarkodina* (35%), *Icriodella* (4%), *Kockelella* (4%) and *Oulodus* (4%). This will be termed the Shelf Biofacies herein. Variations can be seen within the Shelf Biofacies (Aldridge, 1976;

A. Lower Silurian Biofacies



B. Uppermost Ordovician Biofacies



C. Upper Ordovician Biofacies

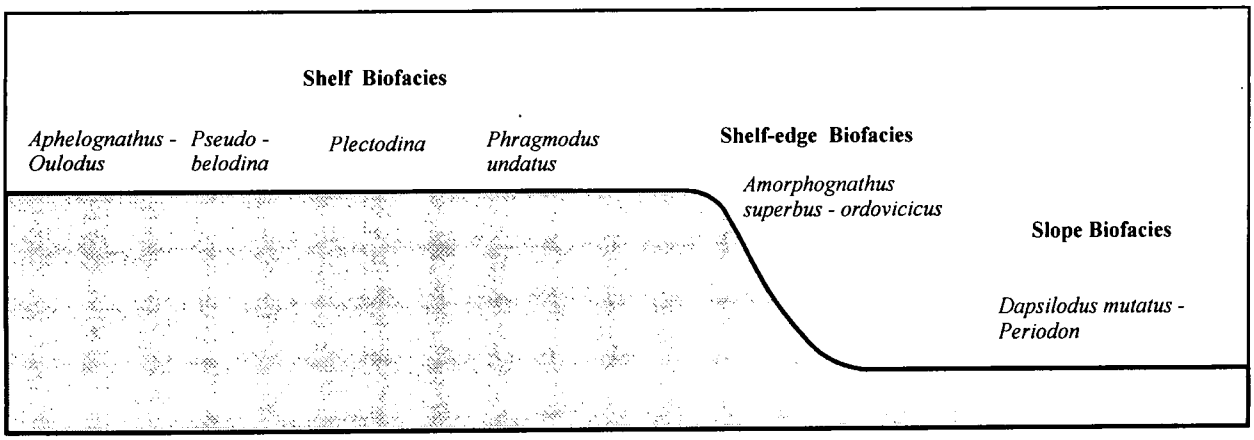


Figure 5.4 Conodont biofacies in the Upper Ordovician to the Lower Silurian around the margins of Laurentia.

Le Fèvre *et al.*, 1976; Aldridge & Mabillard, 1981). For example, *Panderodus* appears to be more dominant in more offshore sections (Section 3.5.2).

The Slope Biofacies was dominated by *Dapsilodus*, *Decoriconus*, *Walliserodus*, *Panderodus* and *Pseudolonchodina* (Armstrong, 1990; McCracken 1991b; Watkins & Kuglitsch, 1997; Herein). It has been observed herein (Section 3.5.2) that the dominant taxa varied through the Llandovery, and this may account for the variations in dominant taxa reported in the literature. For example the fauna recovered by Watkins & Kuglitsch (1997) from the Michigan Basin was dominated by *Panderodus* (58%), *Pseudolonchodina* (13%) and *Walliserodus* (9%). In contrast, McCracken (1991b) identified a fauna dominated by *Walliserodus* (60%), *Pseudolonchodina* (22%), *Dapsilodus* (15%) and *Panderodus* (2%) from the Canadian Cordillera. Throughout the Llandovery, *Pseudolonchodina* is always present and usually dominant within the Slope Biofacies.

In the uppermost Ordovician, a Shelf-edge Biofacies was also detected, which was dominated by coniform taxa (Figure 5.4). The conodont faunas were diverse, with non-coniform taxa only making up a small percentage of the fauna. In the Silurian, the identification of a shelf-edge section has been difficult. The Prongs Creek section, which was regarded as occurring at the shelf-edge in the uppermost Ordovician to lowest Silurian, was in a deeper environment for much of the Llandovery, as a result of rising sea level. Therefore, it is not yet certain whether a Shelf-edge Biofacies, similar to that found in the uppermost Ordovician, also occurred in the Lower Silurian.

Two main biofacies have been identified, but there is evidence that other biofacies may also have existed. For example, a conodont fauna dominated by *Panderodus unicostatus* (74%) and *Walliserodus sancticlairi* (13%) was recovered in shallow-water sediments from high-latitude Gondwana (Spain; Sarmiento *et al.*, 1994; percentages calculated from Sample 10). Other taxa present included *Pseudolonchodina fluegeli* (3%) and *Pseudooneotodus bicornis* (2%). Taxa that comprised less than 1% of the fauna include *Pseudolonchodina 'petila'*, *Dapsilodus obliquicostatus*, *Distomodus* sp., *Oulodus* spp., *Ozarkodina excavata*, *Panderodus*?,

Panderodus langkawiensis and *Panderodus recurvatus* (=*Panderodus panderi*). This fauna indicates that a biofacies dominated by coniforms occurred in cooler water than the Slope Biofacies. This was also suggested by Watkins & Kuglitsch (1997) who recovered samples from the Michigan Basin that only yielded elements of *Panderodus* from deeper-water sediments than the Slope Biofacies. It should be noted that faunas dominated by *Panderodus* may also occur in very shallow water (e.g. Norby *et al.*, 1996), as species of *Panderodus* appear to be Ecological Generalists.

In summary, two main biofacies have been identified in the Llandovery conodont record: Shelf Biofacies and Slope Biofacies. A Shelf-edge Biofacies similar to that observed in the Ordovician has not been identified, possibly due to the lack of studies of conodonts in shelf-edge sections. Other biofacies may also have occurred that have not yet been discovered. For example a biofacies dominated by *Panderodus* and *Walliserodus* may have occurred in higher latitudes and/or cooler water than the Slope Biofacies.

5.2 Pattern of conodont recovery on Laurentia

Detailed study of the initial and long-term recovery of conodonts in sections around Laurentia has allowed the identification of a number of origination/extinction episodes through the uppermost Ordovician and Lower Silurian (Figure 5.5). An initial recovery interval was marked by the first appearance of Silurian-type taxa (*Ozarkodina oldhamensis* and *Distomodus kentuckyensis* Episodes) and was followed by a long-term recovery interval through the Llandovery, during which a number of recovery episodes (origination/emigration episodes) can be identified. These episodes are marked by the first appearance of *Pranognathus tenuis* / *Distomodus staurognathoides*, *Aulacognathus bullatus*, *Pterospathodus celloni* and *Pterospathodus amorphognathoides*. In addition, a Low Diversity Episode has been identified between the *Pranognathus tenuis* and *Aulacognathus bullatus* Episodes.

The bases of the *Pranognathus tenuis* / *Distomodus staurognathoides*, *Pterospathodus celloni* and *Pterospathodus amorphognathoides* Episodes correlate with the bases of internationally recognised conodont biozones (Section 2.3.2). The

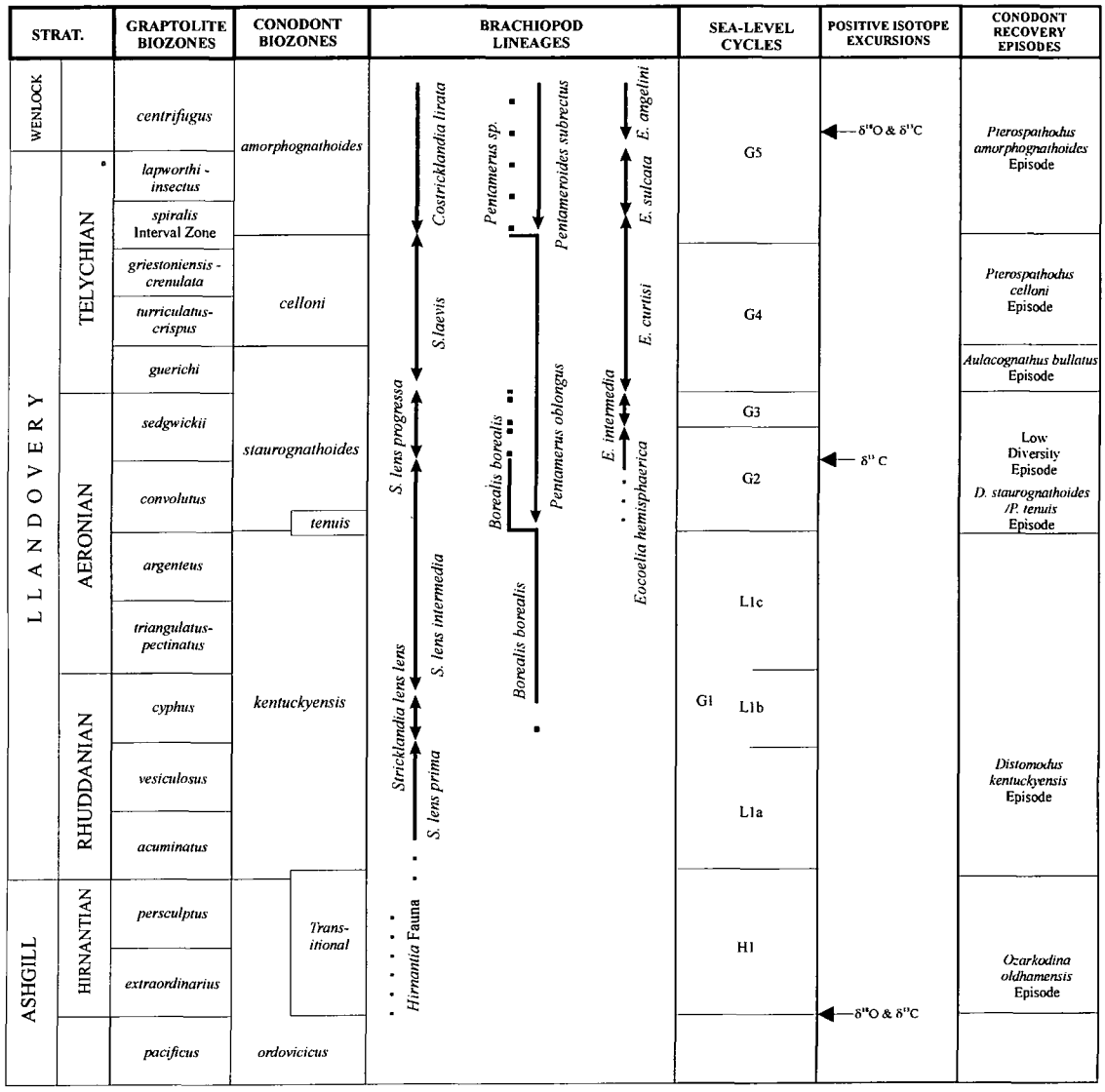


Figure 5.5 The conodont recovery episodes compared with the Upper Ordovician and Lower Silurian stratigraphical framework.

Ozarkodina oldhamensis Episode occurs within the Upper Ordovician *ordovicicus* CBZ, and the Low Diversity and *Aulacognathus bullatus* Episodes occur within the *staurognathoides* CBZ.

The recovery events are also partially comparable to the oceanic episodes and events outlined by Aldridge *et al.* (1993b; Figure 5.2), which were defined using conodont faunal and lithological changes (Section 2.7.2). As has been outlined in Chapter 2, the evidence discussed herein does not support the climatic changes interpreted by Aldridge *et al.* (1993b). For example, Aldridge *et al.* (1993b) interpreted the base of the Jong Primo Episode (*Distomodus staurognathoides* / *Pranognathus tenuis* Episode, herein) as a period of cooling and regression, whereas the evidence reviewed herein suggests that this was actually a period of transgression (Section 2.4.2). Therefore, this study differs from that of Aldridge *et al.* (1993b) in the interpretation of the climatic changes associated with the appearance of new conodont species, and the identification of additional conodont episodes (e.g. *Aulacognathus bullatus* Episode).

The recovery episodes identified herein are defined in terms of the conodont faunas present, sea-level fluctuations and associated macrofossils, and are described in Laurentian sections studied by the author and from the literature. Examples of recovery within the Shelf Biofacies studied herein include the inner-shelf section at Lake Timiskaming (Ontario) and the mid- to outer-shelf Anticosti Island section (Québec; Sami & Deroches, 1992). The outer shelf - slope section at Prongs Creek (Yukon Territories) provides an example of recovery within the Slope Biofacies (Figure 5.6). Correlation, dating and sea-level interpretation of the three successions has been discussed in Chapter 3.

Additional data from the literature is provided by the outer-shelf (Avalanche Lake; Nowlan *et al.*, 1988; Over & Chatterton, 1987a) and trough sections (McCracken 1991b, 1991c) of the Canadian Cordillera. It should be noted that the Prongs Creek section studied herein was deposited in slightly deeper water than the Avalanche Lake section (McCracken, 1989). An example of a deeper-water section adjacent to the Anticosti Island succession occurs in the Percé region of Québec (Nowlan, 1981).

Other examples taken from the literature include the pattern seen on Greenland, where conodonts have been sampled from the platform (Peary Land), platform margin (J.P. Koch Fjord, Wulff Land) and slope (Washington land, Locality 5) environments (Armstrong, 1990).

5.2.1 *Ozarkodina oldhamensis* Episode

This episode is marked by the first appearance of taxa that are common in the early Silurian (Silurian-type taxa). The pattern varies between different environmental settings occurring during the glacial maximum in the Shelf Biofacies and during the post-glacial transgression in the Slope Biofacies.

In the Shelf Biofacies on Anticosti Island, taxa that appear during this episode include *Ozarkodina hassi, Ozarkodina oldhamensis, Oulodus? kentuckyensis, Oulodus? nathani* and *Kockelella manitoulinensis* (Figures 4.7, 4.8, 4.9, 4.10). They appear in a stepwise pattern through the lower Hirnantian, Laframboise Member (O.P.B. and Bioherm Unit) of the Ellis Bay Formation, which has been correlated with the glacial maximum (H1; Correlation discussed in Section 3.3.3). In contrast, the Hirnantian strata (Côte de la Surprise Member of the Whitehead Formation) in the nearby Percé region, yields only elements of *Panderodus,* and Silurian–type taxa first appear in the upper Rhuddanian, L'Irlande Member of the Whitehead Formation (Nowlan, 1981; Figure 4.11). Taxa that disappear within this episode in the Anticosti Island section include *Aphelognathus* aff. *A. grandis, Oulodus ulrichi, Panderodus clinatus, Panderodus* cf. *P. staufferi* and *Plegagnathus nelsoni,* which have not been recorded from strata above the O.P.B. (herein, McCracken & Barnes, 1981, Barnes, 1988). *Amorphognathus ordovicicus, Gamachignathus hastatus, Oulodus robustus, Panderodus gibber* and *Walliserodus* cf. *W. curvatus* do not range above the Bioherm Unit (herein, McCracken & Barnes, 1981, Barnes, 1988). The initial recovery occurs within the period of extinction, during the glacial maximum.

This episode can also be observed in an inner-shelf section in Oklahoma, where the first appearance of Silurian-type taxa occurred within the Hirnantian upper Keel Formation, which has been correlated with the glacial maximum and Global Cycle

H1 (Amsden & Barrick, 1986; Figure 4.6). Taxa that appeared included *Walliserodus curvatus* and *Distomodus* sp. (Amsden & Barrick, 1986). In the inner-shelf section at Missouri studied by McCracken & Barnes (1982), this episode is not observed as the first Silurian-type taxa to appear include *Distomodus kentuckyensis*, which is the index taxon of the following recovery episode (Figure 4.5). Data for the initial recovery in other inner-shelf sections is sparse, as strata of this period is missing in many sections due to hiatuses or lack of exposure (e.g. Lake Timiskaming).

This episode can not been observed within the Slope Biofacies at Prongs Creek, as the first Silurian-type taxa to appear include *Distomodus kentuckyensis*, which is the index taxon of the following recovery episode (Figure 5.6). However, the first appearance of Silurian-type taxa occurs prior to the appearance of *Distomodus kentuckyensis* in the outer-shelf/slope sections of Avalanche Lake (Figure 4.12), Cornwallis Island, Richardson Trough and Dob's Linn, and within strata that can be directly or indirectly correlated with the *persculptus* GBZ (=post-glacial transgression, G1). Taxa that appeared included species of *Ozarkodina* (*Ozarkodina hassi* in Avalanche Lake, *Ozarkodina* sp. A in the Richardson Trough), *Oulodus*? (*Oulodus*? *kentuckyensis* in Cornwallis Island), *Dapsilodus* (*Dapsilodus*? sp. A in Avalanche Lake, *Dapsilodus obliquicosatus* in Dob's Linn), and *Walliserodus* (*Walliserodus curvatus* in Avalanche Lake; Nowlan *et al.*, 1988; Lenz & McCracken, 1988; Melchin *et al.*, 1991; Barnes & Williams, 1988). In the Cornwallis Island, Dob's Linn and Richardson Trough sections the Silurian-type taxa appear in strata which also yield Ordovician-type taxa (Transitional CBZ). However, in the Avalanche Lake section, the Ordovician-type taxa had become extinct prior to the appearance of Silurian-type taxa.

In summary, the current data suggest that the initial recovery was diachronous, occurring in the Slope Biofacies during the post-glacial transgression (G1; *persculptus* GBZ), yet during the glacial maximum (H1; *extraordinarius* GBZ) in the Shelf Biofacies in mid-shelf sections. The taxa that appear in both biofacies at this time are similar, including *Ozarkodina* and *Oulodus*. Exceptions include the occurrence of *Kockelella* in the Shelf Biofacies and *Dapsilodus* in the Slope Biofacies.

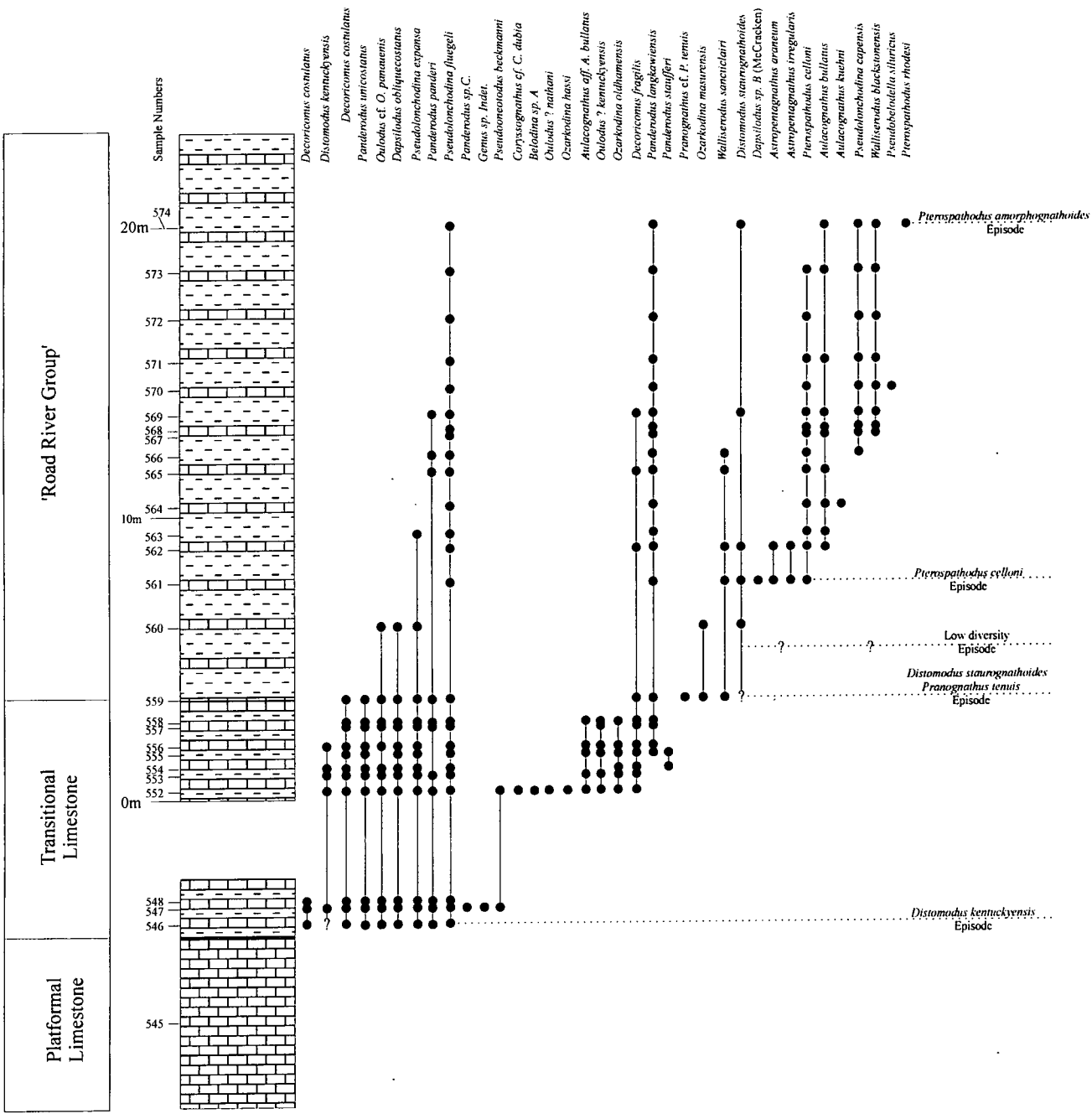


Figure 5.6 Conodont Recovery Events in the Prongs Creek section.

5.2.2 *Distomodus kentuckyensis* Episode

This recovery episode is marked by the first appearance of *Distomodus kentuckyensis* and occurs within the base of Global Cycle G1. The start of this episode heralded the disappearance of all Ordovician-type taxa (except for a few coniform taxa), and a period of relative stasis in conodont diversity through the Lower Llandovery (*kentuckyensis* CBZ).

In the Shelf Biofacies on Anticosti Island, taxa that appear at the base of this episode include *Distomodus* cf. *D. kentuckyensis*, *Icriodella deflecta, Icriodella discreta* and *Walliserodus curvatus,* which appear in the lower part of the Becscie Formation (Figures 4.7, 4.8, 4.9, 4.10). *Ozarkodina pirata, Ozarkodina protoexcavata* and *Oulodus* cf. *O. panuarensis* appear in the upper part of the Becscie Formation. *Ozarkodina protoexcavata* occurs in strata that can be correlated with the *cyphus* GBZ. This species has previously been recovered from northern Michigan – Ontario (Pollock *et al.*, 1970), and southern Ohio (Cooper 1975). An element tentatively assigned to *Pseudolonchodina fluegeli* was recovered from the overlying Merrimack Formation on Anticosti Island, and *Walliserodus sancticlairi* first appeared within the Gun River Formation. Extinctions/disappearances that occurred during this episode include the disappearance of *Oulodus? nathani, Kockelella manitoulinensis, Icriodella discreta* and *Ozarkodina hassi* within the Becscie Formation. The extinction of *Decoriconus costulatus, Distomodus* cf. *D. kentuckyensis, Icriodella deflecta, Oulodus? kentuckyensis, Panderodus gracilis* and *Ozarkodina protoexcavata* occurred within the Gun River Formation.

The section at Percé differs from the other shelf sections in that the basal Llandovery sediments (=40m of L'Irlande Member) have only yielded *Panderodus gracilis* (Nowlan, 1981; Figure 4.11). The first appearance of *Distomodus kentuckyensis* occurs in the upper L'Irlande Member (Whitehead Formation; Nowlan, 1981). Other taxa include *Decoriconus costulatus, Ozarkodina hassi, Walliserodus curvatus* and *Pseudooneotodus beckmanni* (Nowlan, 1981, 1983). The lack of a distinctive fauna in

the basal Llandovery sediments is unknown and could be due to local unfavourable environmental conditions.

The base of this episode can not be identified in the inner-shelf section at Lake Timiskaming, as the basal Llandovery sediments are not exposed. However, it has been observed in an inner-shelf section in Missouri studied by McCracken & Barnes (1982). *Distomodus kentuckyensis* first appear in the Bowling Green Dolomite, which unconformabley overlies Hirnantian strata (Figure 4.5). Other taxa that appear include *Panderodus unicostatus, Walliserodus curvatus, Oulodus? kentuckyensis, Oulodus* cf. *O. nathani, Ozarkodina hassi* and *Ozarkodina oldhamensis* (Figure 4.5). *Pseudooneotodus beckmanni* is the only survivor of the extinction event.

Although the base of this episode can not be seen in the Lake Timiskaming section, a fauna characteristic of the *kentuckyensis* CBZ has been recovered from the Evanturel Creek Formation. Taxa that appear within this episode include *Icriodella deflecta, Icriodella discreta, Kockelella manitoulinensis, Ozarkodina oldhamensis, Ozarkodina hassi, Oulodus petilus, Panderodus acostatus, Panderodus* sp. A and *Decoriconus fragilis* (Figure 3.6). The samples differ from those from Anticosti Island in being dominated by *Icriodella deflecta* and *Icriodella discreta* rather than *Panderodus,* and in the occurrence of *Oulodus petilus*, which does not appear in the Anticosti Island section until the *staurognathoides* CBZ. Other examples of the *kentuckyensis* CBZ fauna can be recorded in the Michigan Basin (Barnes *et al.*, 1978, Norby *et al.*, 1996; Watkins & Kuglitsch 1997) and Hudson Bay Basin (Le Fèvre *et al.*, 1976).

In the Slope Biofacies at Prongs Creek, the first appearance of *Distomodus kentuckyensis* occurs at the base of the transgressive Transitional Limestone Unit (Figure 5.6). Taxa that first appear in the same sample as *Distomodus kentuckyensis* include *Panderodus unicostatus, Pseudolonchodina* sp., *Panderodus panderi, Decoriconus costulatus, Dapsilodus obliquicostatus, Oulodus* cf. *O. panuarensis* and *Walliserodus curvatus*. The taxa continue into the samples immediately above and are joined by *Panderodus* sp. C, Genus sp. Indet. and *Pseudooneotodus beckmanni.*

Above a small gap in the record the Transitional Limestone Unit continues. *Corrysognathus* cf. *C dubia, Oulodus? nathani, Ozarkodina hassi, Pseudooneotodus*

beckmanni and *Belodina* ? sp. A all occur within the basal sample, but are not seen in younger strata. It is interesting to note that *Oulodus*? *nathani*, and *Ozarkodina hassi* are abundant within the Shelf Biofacies in the Rhuddanian. Other taxa that first appear in the basal sample, but continue through the Transitional Limestone Unit, include *Aulacognathus* aff. *A. bullatus*, *Decoriconus fragilis*, *Oulodus*? *kentuckyensis* and *Ozarkodina oldhamensis*. *Panderodus staufferi* and *Panderodus langkawiensis* are the only species that appear within the upper part of the Transitional Limestone Unit.

In the Slope Biofacies at Avalanche Lake, *Distomodus kentuckyensis* first appears within Member 1W of the Whittaker Formation (Over & Chatterton, 1987a). Other taxa that appear include species of *Ozarkodina*, *Icriodella* and *Oulodus*?. These taxa only occur within the middle part of Member 1W, apart from *Ozarkodina hassi*, which extends into the upper part of the member, and is joined by *Oulodus*? *fluegeli* (=*Pseudolonchodina fluegeli*). The Avalanche Lake section was deposited in slightly shallower water than the section at Prongs Creek, which may explain why *Icriodella* has been recovered from this section and not from the Prongs Creek section.

Other examples of the *kentuckyensis* CBZ in the Slope Biofacies have been reported in the Michigan Basin (Watkins & Kuglitsch, 1997), Greenland (Armstrong, 1990) and the Selwyn Basin (McCracken, 1991b). In the platform-edge section at Cornwallis Island, the first appearance of *Distomodus kentuckyensis* can be directly correlated with the *acuminatus* GBZ. Other taxa that appear include *Ozarkodina* cf. *O. hassi* and *Ozarkodina oldhamensis*. The first appearance of species of *Ozarkodina* follows that of *Distomodus kentuckyensis*, which is the reverse of the pattern observed in the Shelf Biofacies.

Distomodus kentuckyensis has not been recovered from any section on Greenland (Armstrong, 1990). The *kentuckyensis* CBZ fauna on the shelf sections of Greenland is similar to that recovered from other localities and includes species of *Ozarkodina*, *Oulodus*, *Kockelella* and *Panderodus*. It differs though in yielding *Pseudolonchodina expansa* and lacking species of *Icriodella*. Samples from the deep-water section in Washington Land (locality 5, fig. 21; Armstrong, 1990), differ from those that occur on the shelf in including *Panderodus* spp. aff. *P. recurvatus* (=*Panderodus* spp. aff.

P. panderi) *Decoriconus fragilis*, *Distomodus* sp., *Dapsilodus obliquicostatus* and *Pseudobelodella*? *siluricus*. The samples also yielded a lower diversity of species of *Oulodus* and *Ozarkodina*.

During this recovery episode, taxa that had appeared during the glacial maximum were joined by additional Silurian–type taxa during the post-glacial transgression (G1). The composition of the faunas varied little through the Rhuddanian to early Aeronian apart from the appearance of a few species of *Ozarkodina*, *Oulodus*, *Panderodus* and *Walliserodus*.

5.2.3 *Pranognathus tenuis* / *Distomodus staurognathoides* Episode

The base of this episode is defined by the first appearance of *Pranognathus tenuis* and / or *Distomodus staurognathoides*. It occurs during the transgressive base of Global Cycle G2. It is associated with the *convolutus* GBZ and the first appearance of *Pentamerus* in shelf sections. It marks the extinction and / or decline of the species indicative of the *kentuckyensis* CBZ and the initiation of the *staurognathoides* and *tenuis* CBZs.

In the Shelf Biofacies at Anticosti Island, the first appearance of *Pranognathus siluricus*, *Pranognathus posteritenuis* and *Distomodus staurognathoides* occurred within the Goéland Member of the Jupiter Formation (Figure 5.7). Their appearance followed the extinction of taxa that were characteristic of the *kentuckyensis* CBZ. Other taxa that appear within this episode include *Pseudolonchodina fluegeli*, *Pseudooneotodus bicornis*, *Decoriconus fragilis*, *Panderodus unicostatus* and *Panderodus staufferi*. The appearance of *Pseudolonchodina fluegeli* at this point within the Shelf Biofacies should be noted, as it first appeared within the Slope Biofacies during the *Distomodus kentuckyensis* Episode. Taxa that became extinct/disappeared in the episode included *Pranognathus siluricus* and *Ozarkodina oldhamensis*.

This episode has not been identified in the inner-shelf, Lake Timiskaming section, possibly due to the lack of continuous sampling through the section. It has been noted

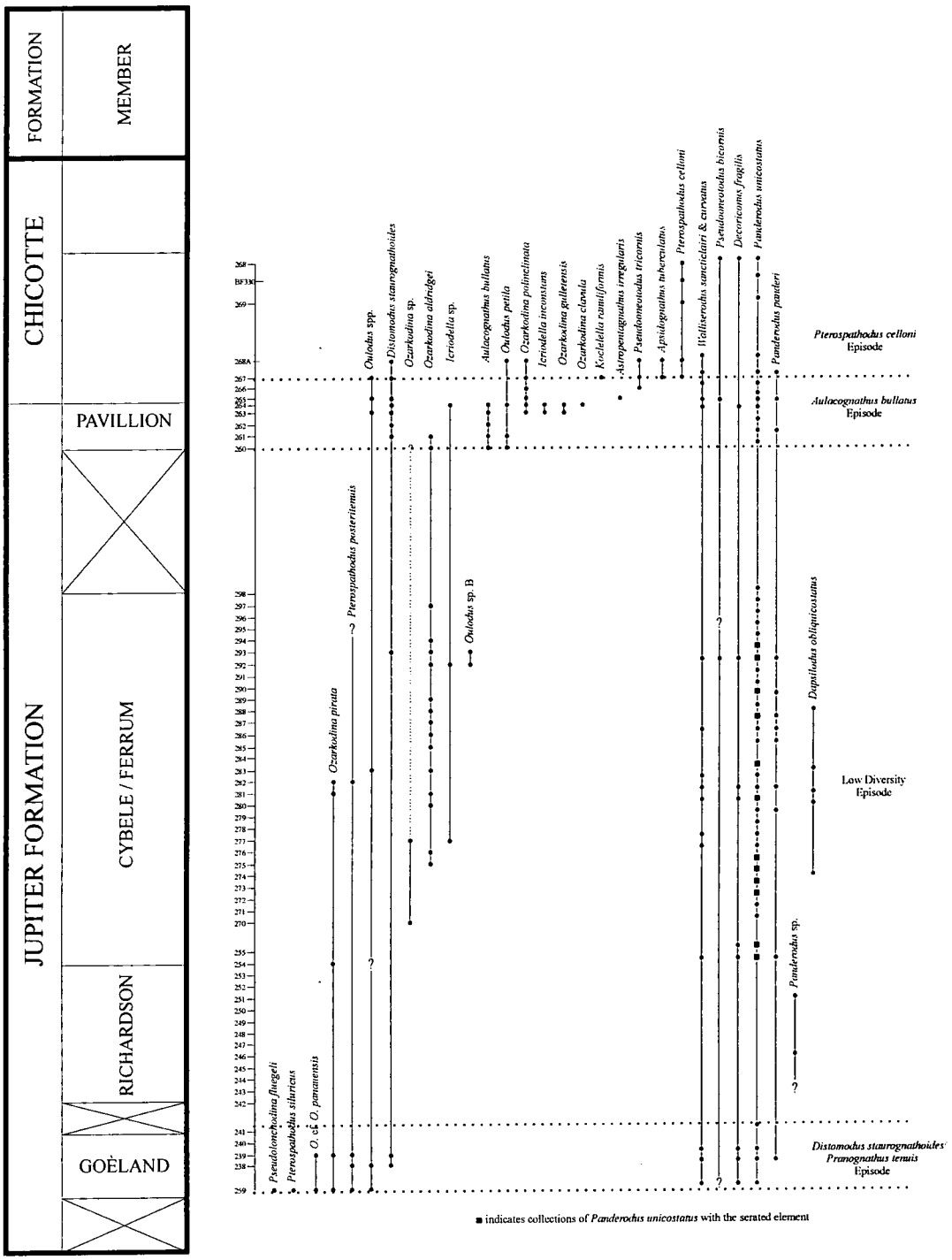


Figure 5.7 Conodont Recovery Events in the Jupiter Formation of Anticosti Island shown by the range data from Uyeno & Barnes (1983). A number of the species names have been updated.

by other authors that conodont taxa indicative of the *staurognathoides* CBZ have not been identified in inner-shelf successions on the American Midcontinent (Norby *et al.*, 1996). However, species of *Pranognathus* have been recovered from Northern Michigan and Ontario (Pollock *et al.*, 1970; Cooper, 1977). Examples of the *Distomodus staurognathoides* CBZ fauna have been recorded in the Michigan Basin (Nicoll & Rexroad, 1969). The pattern in this section is different than that seen in the Anticosti Island section in that taxa indicative of the *kentuckyensis* CBZ are found in association with taxa of the *staurognathoides* CBZ. For example, *Distomodus staurognathoides* occurs with conodonts indicative of the *kentuckyensis* CBZ within the basal part of the Brassfield Limestone (Nicoll & Rexroad, 1969; Cooper, 1980), and *Pranognathus siluricus* and *Pranognathus tenuis* with elements of the *kentuckyensis* CBZ (e.g. *Icriodella discreta*) occur within the Neahga shale (Niagara Falls).

Pranognathus tenuis and the *staurognathoides* CBZ had not been identified in the Slope Biofacies of northwestern Canada (e.g. McCracken, 1991b). For example, in the Avalanche Lake section only *Pseudolonchodina fluegeli* had been recovered from Member 2W of the Whittaker Formation (Over & Chatterton, 1987a). However, at Prongs Creek, *Pranognathus* cf. *P. tenuis* has been recovered from the uppermost bed of the Transitional Limestone Unit. Its appearance coincides with the disappearance of many species characteristic of the underlying fauna. Other taxa that appear at this point include *Ozarkodina masurensis*, *Walliserodus sancticlairi* and *Distomodus staurognathoides*?. *Ozarkodina masurensis* has not been previously recovered from Laurentia, but has been recovered from low-latitude Gondwana (Australia Bischoff, 1986; Section 5.3.3), where it occurs in association with '*Pterospathodus' cadiaensis*.

In the Greenland sections, species of *Pranognathus* are lacking. The first appearance of *Distomodus staurognathoides* only occurs prior to the *celloni* CBZ in the shelf-edge section at J.P. Koch Fjord. In this section, the appearance of *Distomodus staurognathoides* occurs in slightly younger strata than the appearance of *Pseudolonchodina fluegeli* within the Washington Land Group. Other taxa that appear include *Walliserodus curvatus* and *Ozarkodina pirata*. The appearance of *Aspelundia fluegeli* (=*Pseudolonchodina fluegeli*) coincides with the extinction of a

number of species of *Ozarkodina* (e.g. *Ozarkodina hassi*) and *Oulodus* in the shelf and shelf-edge sections, and the disappearance of *Aspelundia expansa* (=*Pseudolonchodina expansa*), *Dapsilodus obliquicostatus* and *Decoriconus fragilis* in the slope section. Other taxa that first appear at the same time as *Aspelundia fluegeli* (=*Pseudolonchodina fluegeli*) include *Panderodus recurvatus* (=*Panderodus panderi*) and *Panderodus* aff. *P. recurvatus* (=*Panderodus* aff. *P. panderi*) and a number of species of *Ozarkodina* and *Oulodus* in open nomenclature appear in the Odin Fjord Formation. In the deep-water section (Washington Land, locality 5, fig. 21; Armstrong, 1990), the appearance of *Aspelundia fluegeli* (=*Pseudolonchodina fluegeli*), occurs in association with the first appearance of *Walliserodus bicostatus* (=*Walliserodus blackstonesis*) and *Walliserodus* cf. *W. sancticlairi* in the Cape Schuchert Formation.

At the initiation of this episode, the faunal elements of the *kentuckyensis* CBZ declined or became extinct and were replaced by the *staurognathoides* and *tenuis* CBZ fauna. Transgression at the base of Global Cycle G2 saw the appearance of the new taxa on to the shelf. Taxa that first appeared within the Slope Biofacies at the base of the Llandovery, such as *Pseudolonchodina fluegeli*, first appeared in the Shelf Biofacies during this episode.

5.2.4 Low Diversity Episode

The basal part of this episode is characterised by the disappearance of the fauna indicative of the *tenuis* CBZ and the establishment of a low diversity and low abundance conodont fauna. The basal part of the episode is coincident with the regressive phase of Global Cycle G2 and a positive $\delta^{13}C$ isotope excursion (Wenzel, 1996; Heath *pers. comm.*). The remainder of the episode correlates with Global Cycle G3. The episode occurs within the *sedgwickii-halli* GBZs and in the Shelf Biofacies it is associated with the presence of the brachiopod *Pentamerus oblongus*.

In the Shelf Biofacies on Anticosti Island, *Pranognathus tenuis* disappeared within the upper Goéland Member of the Jupiter Formation. A low-diversity fauna occurred within the overlying regressive (upper part of Global Cycle G2) East Point Member (Jupiter Formation), characterised by *Decoriconus costulatus*, *Ozarkodina pirata*,

Panderodus acostatus and *Walliserodus curvatus*. The extinction of *Oulodus* cf. *O. panuarensis* and *Pseudooneotodus beckmanni* occurred within the East Point Member. Only rare *Panderodus* elements were recovered from the overlying Richardson Member (Uyeno & Barnes, 1983; Figure 5.7), which has been correlated with the transgressive part of Global Cycle G3 (Section 3.5.1). Diversity increased again in the overlying, regressive Cybéle Member, which yields graptolites indicative of the *sedgwickii* GBZ (Riva, 1981). The conodont fauna includes *Panderodus unicostatus* (with serrate elements; Uyeno & Barnes, 1983). New taxa, which appeared in a stepwise pattern included *Ozarkodina* sp., *Dapsilodus obliquicostatus*, *Ozarkodina aldridgei* and *Icriodella* sp. (Uyeno & Barnes, 1983). *Pranognathus posteritenuis* briefly reappears within one sample. It is interesting to note that *Dapsilodus obliquicostatus* first appeared in the Slope Biofacies within the *kentuckyensis* CBZ. Taxa that became extinct/disappeared within the Cybéle and Ferrum Members included *Ozarkodina pirata*, *Pranognathus posteritenuis*, *Dapsilodus obliquicostatus* and *Oulodus* cf. *O. masurensis*.

In many of the Midcontinent sections, a major unconformity occurs between strata of the *staurognathoides* CBZ and strata of the *celloni* CBZ. For example, unconformities have been recorded from Indiana, Kentucky (Nicoll & Rexroad, 1969), Illinois, Wisconsin (Kluessendorf & Mikulic, 1996), Michigan and Ontario (Pollock *et al.*, 1970). A major unconformity has not been detected in the inner-shelf, Lake Timiskaming section, but this episode has not been located within that section due to the lack of continuous sampling. A non-diagnostic fauna was recovered from ostracode-rich limestones within the Earlton Formation, interpreted by Colville & Johnson (1982) as regressive. The fauna is dominated by *Kockelella* sp. B, *Ozarkodina* cf. O. sp. C Armstrong and *Panderodus unicostatus*. A new species of *Panderodus*, *Panderodus* sp. B, occurs in one sample, and *Oulodus petilus* continues from older strata.

This episode has not been conclusively identified within the Slope Biofacies. In the Prongs Creek section, the sample from strata (basal Road River Group) directly above the *tenuis* CBZ yielded *Pseudolonchodina fluegeli* and *Dapsilodus obliquicostatus*, *Ozarkodina masurensis*, *Distomodus* sp. and *Oulodus* cf. *O. panuarensis,* which had all continued from strata below. In the Avalanche Lake section, only elements of

Pseudolonchodina fluegeli could be recovered from strata between those containing elements of the *kentuckyensis* CBZ and those of the *celloni* CBZ (Over & Chatterton, 1987a).

The pattern on Anticosti Island indicates that within the Shelf Biofacies, taxa indicative of the preceding episode become extinct / disappear during the regressive phase of Global Cycle G2 and are replaced by a fauna including *Ozarkodina* and coniform taxa. This is followed by a transgression during Global Cycle G3 and the appearance of conodont faunas comprising exclusively simple cones. During the subsequent regression diversity increased and *Dapsilodus* appeared for the first time in the Shelf Biofacies. This episode has not been conclusively identified within the Slope Biofacies.

5.2.5 *Aulacognathus bullatus* Episode

This recovery episode is defined by the first appearance of *Aulacognathus bullatus* in sections were it precedes the first appearance of *Pterospathodus celloni*. The base corresponds to the transgressive base of Global Cycle 4a. This episode can be correlated with the *guerichi* GBZ and the appearance of *Eocoelia curtisi* in shelf sections. *Pentameroides* may also first appear during this episode, although the diachronous nature of its first appearance has been demonstrated (Colville & Johnson, 1982; Section 2.3.3).

In the Shelf Biofacies on Anticosti Island, *Aulacognathus bullatus* appeared at the base of the Pavillion Member of the Jupiter Formation, which has been correlated with Global Cycle 4a (Figure 5.8). *Ozarkodina polinclinata*, *Icriodella* cf. *I. inconstans*, *Ozarkodina gulletensis*, *Ozarkodina clavula*, *Astropentagnathus irregularis* and *Kockelella ranuliformis* appeared in a stepwise pattern within the Pavillion Member. The extinctions of *Ozarkodina aldridgei*, *Icriodella* cf. *I. inconstans*, *Ozarkodina clavula* and *Pseudooneotodus* sp. A occurred within the Pavillion Member. This episode was not identified in the inner-shelf, Lake Timiskaming section. In fact, it has not been recorded on any of the inner-shelf sections that have been discussed in the literature.

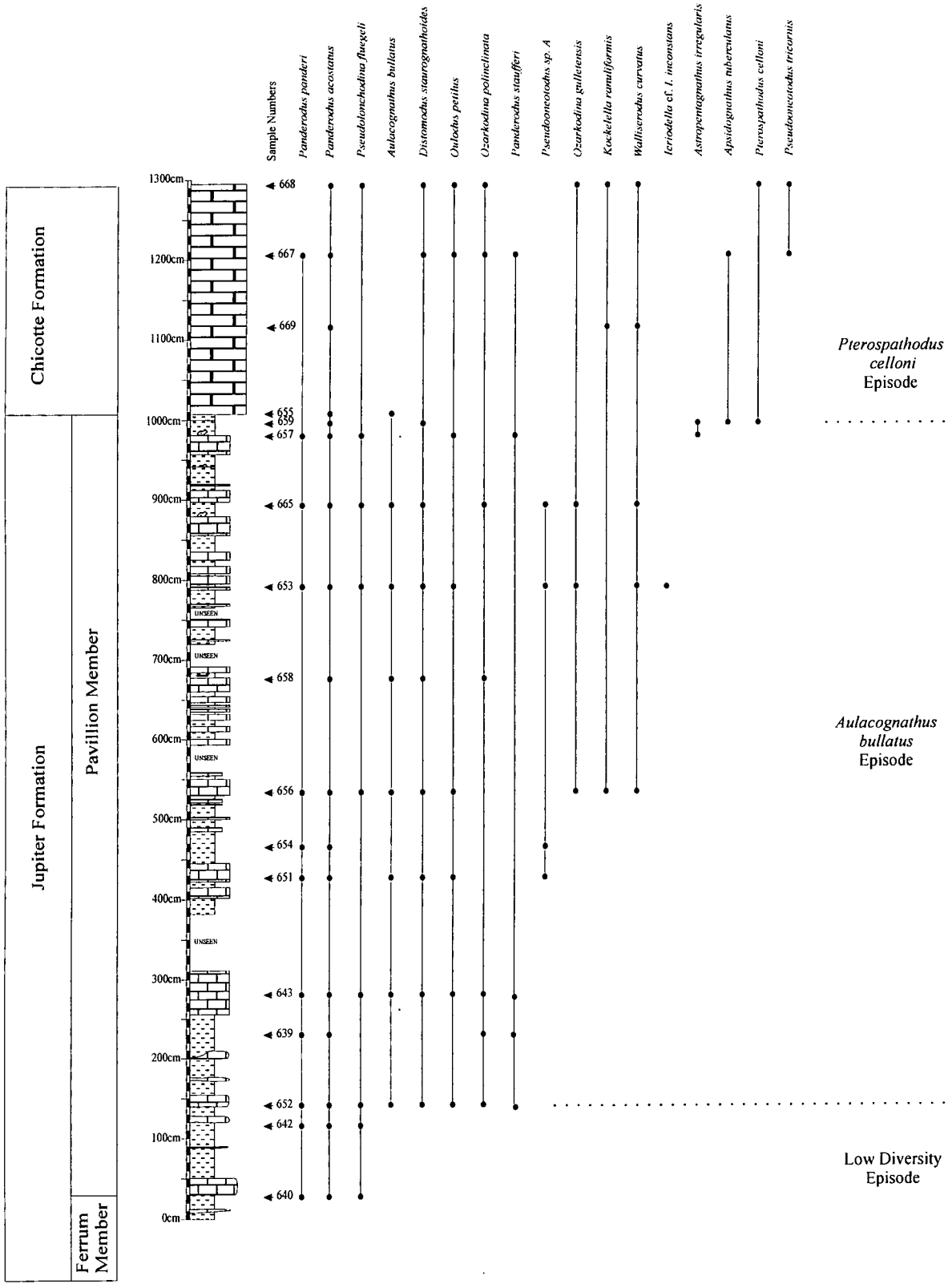


Figure 5.8 Conodont recovery episodes observed at the Brisants Jumpers section, Anticosti Island (Locality AI 5).

The only other section on Laurentia where *Aulacognathus* precedes the first appearance of *Pterospathodus celloni* occurs in a shelf section on Greenland (Armstrong, 1990). Within the upper Odin Fjord Formation, *Aulacognathus bullatus* first appears along with *Kockelella manitoulinensis*, *Panderodus greenlandensis* (=*Panderodus staufferi*) and *Panderodus unicostatus*, which had continued from older strata. *Belodina cooperi* and *Pseudolonchodina fluegeli* also made their first appearances in this section immediately prior to the appearance of *Pterospathodus celloni*. *Kockelella manitoulinensis* is the only species that does not range up into the *celloni* CBZ (see Armstrong, 1990, fig. 7). In other shelf sections on Laurentia, *Kockelella manitoulinensis* has not been identified above the basal part of the *kentuckyensis* CBZ.

The appearance of *Aulacognathus bullatus* prior to the appearance of *Pterospathodus celloni* has been found associated with Global Cycle G4a in the Shelf Biofacies on Anticosti Island and Greenland. On Anticosti Island, a number of species of *Ozarkodina* first appear within this episode. The episode has not been recorded in the Slope Biofacies though.

5.2.6 *Pterospathodus celloni* Episode

This episode is marked by the first appearance of *Pterospathodus celloni* (*celloni* CBZ) and can be correlated with the transgressive base of Global Cycle G4b. The base of this episode occurs within the *turriculatus-crispus* GBZ.

On Anticosti Island, *Pterospathodus celloni* first appears at the boundary between the Jupiter and Chicotte Formations (Figure 5.8), along with *Apsidognathus tuberculatus*. *Pseudooneotodus tricornis*, *Panderodus langkawiensis* and *Ozarkodina excavata* appear slightly higher within the Chicotte Formation. *Distomodus staurognathoides*, *Oulodus petilus* and *Ozarkodina polinclinata* continue from the Pavillion Member below. Long (1996) identified regression at the base of the Chicotte Formation followed by a subsequent rise, possibly correlating with Global Cycle 4b.

In the inner-shelf, Lake Timiskaming section, *Pterospathodus celloni* has not been recovered. However, *Pterospathodus*? sp. A and *Aulacognathus bullatus* were recovered from the basal beds of the Thornloe Formation, interpreted as transgressive by Colville & Johnson (1982; Global Cycle G4b). The appearance of a species of *Pterospathodus* may indicate correlation with this episode, but the relationship between *Pterospathodus celloni* and *Pterospathodus*? sp. A needs to be investigated (Appendix A). Other species present included *Ozarkodina gulletensis*, *Ozarkodina polinclinata* and *Panderodus panderi*. Taxa that appeared in younger samples within the Thornloe Formation include *Aulacognathus* sp. A, *Panderodus staufferi*, *Walliserodus curvatus*, *Ozarkodina* sp. A and *Kockelella* sp. A (Over & Chatterton). *Oulodus petilus* and *Panderodus unicostatus* continued from older strata.

Examples of the *celloni* CBZ fauna have been recorded in the Michigan Basin (Kleffner *et al.*, 1994; Kluessendorf & Mikulic, 1996) and Hudson Bay Basin (Le Fèvre *et al.*, 1976). In Illinois and Wisconsin (Michigan Basin), the argillaceous sediments deposited during the *celloni* CBZ represent a basal transgressive systems tract onlapping on to Aeronian strata (Kluessendorf & Mikulic 1996). *Pterospathodus celloni* appears within the Lee Creek Member of the Brassfield Limestone Formation, which is transgressive (Nicoll & Rexroad, 1969).

In the shelf sections of Greenland, taxa that first appear alongside *Pterospathodus celloni* include species that occur in other sections at this point. They include species of *Ozarkodina, Aulacognathus, Apsidognathus, Pseudooneotodus, Panderodus, Astropentagnathus, Distomodus, Kockelella* and *Walliserodus*. The extinction of a number of species of *Ozarkodina* and *Oulodus* in open nomenclature, *Panderodus* aff. *P. greenlandensis* (=*Panderodus* aff. *P. staufferi*), and Genus and Sp. indet A and B occurred prior to the appearance of *Pterospathodus celloni. Pseudobelodella siluricus* also appears, which has not been recovered from other shelf sections. It is interesting to note that *Dapsilodus obliquicostatus* continues into the *celloni* CBZ in Greenland, as it disappeared just below the *celloni* CBZ in the Anticosti Island (Shelf Biofacies) and Prongs Creek (Slope Biofacies) sections.

In the deeper section at Washington Land (locality 5, fig. 21; Armstrong, 1990), *Pterospathodus celloni* first appears within the basal Lafayette Bugt Formation. Other

taxa that first appear include *Belodella cooperi*, *Panderodus* aff. *P. spasovi* (=*Panderodus* aff. *P. langkawiensis*) and *Pseudoneotodus* sp.. *Walliserodus bicostatus* (=*Walliserodus blackstonensis*) did not continue into the *celloni* CBZ from the strata below.

Within the Slope Biofacies at Prongs Creek, the first appearance of *Pterospathodus celloni* occurs just above a level where graptolites of the *guerichi – turriculatus-crispus* GBZs have been recovered (McCracken, 1989). This allows correlation with the lower part of the Global Cycle G4. In addition to the index taxon, the basal samples contain *Astropentagnathus araneum*, *Astropentagnathus irregularis*, and *Dapsilodus*? sp. B. *Aulacognathus bullatus, Aulacognathus kuenhi*, *Pseudolonchodina capensis*, *Walliserodus blackstonensis* and *Pseudobelodina siluricus* appear in a stepwise pattern through the *celloni* CBZ. It is important to note that *Pseudolonchodina capensis* replaces *Pseudolonchodina fluegeli* as the dominant species of *Pseudolonchodina* within this episode. Elements assignable to Pseudolonchodina *capensis* had occurred in older strata, but the full apparatus was not recognised/dominant before this episode. *Dapsilodus*? sp. B McCracken, which was recovered from sample PC 561, has previously been recovered from the *gregarius* and *turriculatus* GBZs in the Canadian Cordillera (McCracken, 1991b). It is the last representative of the Genus *Dapsilodus* in this section. The conodont species from the samples below continue through the *celloni* CBZ, apart from species of *Astropentagnathus* and *Dapsilodus*, which only occur in the basal samples.

Other examples of the *celloni* CBZ in the Slope Biofacies are available from the Mackenzie Mountains (McCracken, 1991b, 1991c) In the Avalanche Lake section, *Pterospathodus celloni* first appears at the base of Member 3W (Whittaker Formation; Over & Chatterton, 1987a). Taxa that also occur within the Prongs Creek section include *Astropentagnathus irregularis, Aulacognathus b. bullatus Distomodus staurognathoides* and *Pseudolonchodina fluegeli.* Additional taxa include *Astrolecignathus milleri* and *Ozarkodina gulletensis.* The appearance of *Ozarkodina* in this section may again reflect the slightly shallow location of this section compared to Prongs Creek. Samples of the *celloni* CBZ from the trough sections Blackstone River, Telit Creek and Rock River sections (Canadian Cordillera) yielded many of the

taxa recovered from the *celloni* CBZ at Prongs Creek. However, the samples differed in yielding elements of *Ozarkodina* and *Oulodus* (McCracken, 1991b).

Pterospathodus celloni first appears during Global Cycle G4b. Taxa that appear in both biofacies at the base of this episode include *Pterospathodus celloni* and *Astropentagnathus irregularis*. The evolution of *Pseudolonchodina capensis* from *Pseudolonchodina fluegeli* occurred within the Slope Biofacies, which lacked species of *Ozarkodina* and *Oulodus*.

5.2.7 *Pterospathodus amorphognathoides* Episode

This episode is characterised by the first appearance of *Pterospathodus amorphognathoides* and can be correlated with the transgressive base of Global Cycle G5 (*spiralis* GBZ). In some sections, *Pterospathodus celloni* is replaced by *Pterospathodus rhodesi* instead of *Pterospathodus amorphognathoides*. The first appearance of *Pterospathodus rhodesi* is used to define the base of the *amorphognathoides* CBZ in such sections.

Sediments of this age were not sampled for conodonts in the inner-shelf, Lake Timiskaming section. The *amorphognathoides* CBZ has also not been conclusively identified in the Anticosti Island succession (Section 3.3.2b). However, examples of the *amorphognathoides* CBZ fauna have been found in other Laurentian sections including those in the Michigan Basin (Kleffner *et al.*, 1994; Kluessendorf & Mikulic, 1996), Hudson Bay Basin (Le Fèvre *et al.*, 1976) and Greenland (Armstrong, 1990).

In the Shelf Biofacies of Greenland, the first appearance of *Pterospathodus amorphognathoides* has been recorded from the Samuelsen Høj Formation (Kronprins Christian Land; Armstrong 1990; fig. 9). *Walliserodus* cf. *W. sancticlairi* is the only species to first appear within the same horizon as *Pterospathodus amorphognathoides*. *Pseudooneotodus tricornis* became extinct just below the first appearance of *Pterospathodus amorphognathoides*.

Within the Slope Biofacies at Prongs Creek, the first appearance of conodonts indicative of the *amorphognathoides* CBZ (*Pterospathodus rhodesi*) is within the *spiralis* GBZ (Figure 5.6). *Pterospathodus rhodesi* is the only species to first appear at this horizon. Taxa that continue from below include *Panderodus langkawiensis*, *Pseudolonchodina* sp., *Walliserodus blackstonensis*, *Aulacognathus bullatus* and *Distomodus staurognathoides*. In the nearby Avalanche Lake section, a more diverse fauna appeared in conjunction with the first appearance of *Pterospathodus amorphognathoides* and *Pterospathodus p. rhodesi* at the base of Member 3W (Whittaker Formation; Over & Chatterton, 1987a). The fauna included species of *Oulodus* (*Oulodus*? sp. 1 and 2), *Apsidognathus* (*Apsidognathus tuberculatus, Apsidognathus barbarajeanae*), *Aulacognathus* (*Aulacognathus kuehni, Aulacognathus chapini*), *Astrolecignathus* (*Astrolecignathus newti*), *Ozarkodina* (*Ozarkodina hadra*) and *Kockelella* (*Kockelella ranuliformis*). The taxa from the *celloni* CBZ continued into this strata.

In the deep-water section in Greenland (Washington Land; locality 5, fig. 21 of Armstrong, 1990) a diverse fauna was also recovered. *Pterospathodus amorphognathoides* first appears within the upper Lafayette Bugt Formation, along with species of *Apsidognathus*, *Ozarkodina*, *Dentacodina, Panderodus* and *Walliserodus*. These taxa had first appeared within the *celloni* zone in the shelf sections on Greenland. Other examples of the *amorphognathoides* CBZ in the Slope Biofacies occur in the Canadian Cordillera (Over & Chatterton, 1987a; McCracken, 1991) and Alaska (Savage, 1986).

This episode is marked by the appearance of *Pterospathodus amorphognathoides* in the Shelf and Slope Biofacies during Global Cycle G5. *Pterospathodus amorphognathoides* replaces *Pterospathodus celloni* as the dominant form of that species.

5.2.8 Summary of pattern on Laurentia

The initial recovery within the Shelf Biofacies occurred during a minor sea-level rise within the glacial maximum (H1). The first taxa to appear include *Ozarkodina hassi*,

Ozarkodina oldhamensis, *Kockelella manitoulinensis*, *Oulodus*? *nathani* and *Oulodus*? *kentuckyensis*. Silurian-type taxa appear within the glacial maximum along with Ordovician-type taxa (Transitional CBZ). Within the Slope Biofacies, the first appearance of Silurian-type taxa occurred during the post-glacial transgression within the *persculptus* GBZ. This indicates that recovery occurred slightly later in the Slope Biofacies than in the Shelf Biofacies and that the initial recovery was diachronous.

Transgression continued in the *acuminatus* GBZ and *Distomodus kentuckyensis* first appeared during Global Cycle G1. The disappearance of all Ordovician-type taxa (except for a few coniforms) also occurred. A period of relative stasis in conodont diversity ensued through the lower Llandovery (*kentuckyensis* CBZ). The *kentuckyensis* CBZ fauna varies little. In the Shelf Biofacies, the appearance of *Ozarkodina protoexcavata* within the *cyphus* GBZ coincides with a sea-level rise (Laurentian Cycle L1b).

During the mid Aeronian transgression (Global Cycle G2; *convolutus* GBZ), species of *Pranognathus* appeared within the Slope and Shelf Biofacies. In shelf sections elements of the Slope Biofacies, such as *Pseudolonchodina fluegeli* appeared in the Shelf Biofacies. The extinction/disappearance of *Pranognathus tenuis* and the elements of the Slope Biofacies that had appeared in the Shelf Biofacies were associated with the upper regressive part of Global Cycle G2. A major sea-level fall occurred at this time, which resulted in unconformities in many shallow sections. A positive $\delta^{13}C$ excursion has been identified in the basal *sedgwickii* GBZ (Wenzel, 1996; Heath *pers. comm.*), which may indicate cooling (Section 2.5).

During the basal transgression of Global Cycle G3 (upper *sedgwickii* GBZ), the conodont fauna in mid-shelf successions became dominated by *Panderodus* (e.g. Anticosti Island). The following regression saw the appearance of *Dapsilodus* in the Shelf Biofacies and in some areas the reappearance of *Pranognathus*. During the basal transgression of Global Cycle G4a (*guerichi* GBZ), *Aulacognathus* appears within the Shelf Biofacies. The appearance of *Aulacognathus bullatus* prior to the appearance of *Pterospathodus celloni* has not yet been identified in the Slope Biofacies.

The appearance of *Pterospathodus celloni* in the Shelf and Slope Biofacies occurred during the transgressive base of Global Cycle G4b (*turriculatus-crispus* GBZ). *Pterospathodus celloni* appeared in shelf and slope areas along with a number of other prioniodontid species, such as *Astropentagnathus* (appears at the base of the event) and *Apsidognathus*. The Pterospathodontids remained established on the shelf during the following regressive phase and the next transgression (Global Cycle G5; *spiralis* GBZ) saw the appearance of *Pterospathodus amorphognathoides*.

5.3 Pattern of recovery on other palaeocontinents

The palaeogeographic reconstruction for the Llandovery followed herein is that of Bergström (1990). North America, north-western Europe and Siberia were close neighbours around the margins of the Iapetus Ocean within the tropics. South China and Australia were situated within the tropics on the opposite side of the Rheic Ocean to Baltica. Southwest Europe was attached to Gondwana in high latitudes. The identification of the Llandovery recovery episodes, using data from the literature, on palaeocontinents other than Laurentia is discussed below.

Conodont studies have been conducted through Upper Ordovician and Lower Silurian strata on Avalonia (Britain by Aldridge, 1972), Baltica (Oslo Graben by Aldridge & Mohammed, 1982), low-latitude Gondwana (Australia by Bischoff, 1986), and high-latitude Gondwana (Spain by Sarmiento *et al.*, 1994). The sections in Avalonia and Baltica provide examples of the Shelf Biofacies. The biofacies present within the Australian section is difficult to determine, as Bischoff (1986) did not discuss the coniform genera recovered. The lack of *Icriodella* and the appearance of *Pseudolonchodina fluegeli* through the section suggests affinity with the Slope Biofacies.

Unfortunately, the conodont data for most of the sections on palaeocontinents other than Laurentia is not continuous, and so it is difficult to record the exact first appearances or disappearances of taxa. For example, the data from high-latitude Gondwana (Spain) is restricted to the *kentuckyensis* CBZ (Sarmiento *et al.*, 1994).

Conodont sampling through the section on low-latitude Gondwana (Australia) was relatively continuous, but there are a number of unconformities within the section (Bischoff, 1986). The presence of these unconformities coupled with the fact that Bischoff (1986) did not include coniform taxa in his study, results in an incomplete record of recovery. Simpson (1995) also suggested that some of the samples collected by Bischoff (1986) had been incorrectly dated and cast doubt on the correlation of the sections in New South Wales with graptolitic biozones by Jell & Talent (1989)

The identification of recovery episodes within the Chinese sections has not been documented herein as it is difficult to relate the sections to the biostratigraphic framework utilised herein. Sea-level interpretations of the section have been published by Johnson *et al.* (1991a) and Johnson (1996), but as discussed by Loydell (1998) the formations within those studies were incorrectly correlated and dated (Section 2.4).

5.3.1 *Ozarkodina oldhamensis* Episode

There is a general lack of conodont studies of Upper Ordovician to Lower Silurian sections on palaeocontinents other than Laurentia. Only one section which is situated on Baltica (Sweden) has been thoroughly sampled (Bergström & Bergström, 1996). The Hirnantian Loka Formation is overlain by the Motala Formation. This first appearance of Silurian-type taxa occurs within the Hirnantian Loka Formation (Bergström & Bergström, 1996). The Silurian-type taxa include *Walliserodus curvatus* and *Ozarkodina* sp. and appear in strata bearing the Ordovician-type taxa (Transitional CBZ). Limited data from the Oslo Graben also indicates that the first appearance of *Ozarkodina* aff. *O. oldhamensis* has been recorded within Hirnantian strata (Aldridge & Mohammed, 1982; Barnes & Bergström, 1988). Therefore, the initial recovery has also been identified within the glacial maximum in Baltic sections, as it has been in Laurentian mid-shelf sections.

5.3.2 *Distomodus kentuckyensis* Episode

The first appearance of *Distomodus kentuckyensis* has been reported from sections on Baltica (Norway and Sweden). The first appearance has not been documented on Avalonia (Britain) or low- and high-latitude Gondwana (Australia and Spain), but examples of the *kentuckyensis* CBZ fauna have been recovered from those areas.

On Baltica the first appearance of *Distomodus kentuckyensis* occurs within the Motala Formation of Sweden, which unconformabley overlies Hirnantian sediments (Bergström & Bergström, 1996). It has also been observed within the Solvik Formation of Norway (Idris, 1983). Common taxa between the two sections include *Icriodella discreta*, *Dapsilodus obliquicostatus*, and *Ozarkodina oldhamensis*. *Aspeludia fluegeli* (=*Pseudolonchodina fluegeli*) has been recorded from the uppermost part of the Motala Formation (Bergström & Bergström, 1996). The *kentuckyensis* CBZ fauna recovered from Baltica is very similar in composition to that recovered from Laurentia. It yields species of *Icriodella, Oulodus*?, *Oulodus*., *Ozarkodina, Panderodus, Pseudooneotodus* and *Walliserodus* (Aldridge & Mohammed 1982; Idris, 1983).

The fauna recovered from a section on high-latitude Gondwana (Spain), differs from the fauna recovered on Baltica and Laurentia in being dominated by *Walliserodus* and *Panderodus*. Species typical of the Shelf Biofacies on Laurentia are present in small numbers and include species of *Oulodus*, *Ozarkodina*, *Pseudooneotodus*, *Kockelella*, *Distomodus* and *Decoriconus*. However, taxa typical of the Laurentian Slope Biofacies have also been recovered: *Oulodus petilus* (=*Pseudolonchodina expansa*), *Aspelundia fluegeli* (*Pseudolonchodina fluegeli*), *Panderodus langkawiensis* and *Dapsilodus obliquicostatus* (Sarmiento *et al.*, 1994).

On low-latitude Gondwana (Australia), the Upper Ordovician to basal Silurian hiatus is overlain by the transgressive, Baghdad Formation (*vesiculosus* to basal *cyphus* GBZ), which yields a conodont fauna including largely endemic species of *Distomodus*, *Oulodus*, *Ozarkodina* and *Pseudooneotodus* (Bischoff, 1986; Simpson, 1995).

5.3.3 *Pranognathus tenuis / Distomodus staurognathoides* Episode

The first appearance of *Pranognathus* has been recorded in the basal *Pentamerus* Beds of Britain (Avalonia; Aldridge, 1972; Aldridge *et al.*, 1993b; Loydell, 1998), the uppermost Solvik Formation of Norway (Baltica; *convolutus* GBZ; Worsley, 1989) and in the Vodopod Formation of Severnaya Zemlya (Siberia; Männik, 1983)

The first appearance of *Pranognathus* is associated with the first appearance of *Distomodus* aff. *D. staurognathoides* and elements of *Panderodus* with serrate elements in the British and Norwegian sections (Aldridge & Mohammed, 1982; Aldridge *et al.*, 1993b). In the British section, *Panderodus panderi* occurs and in the Norwegian section it increases in abundance at this point (Aldridge & Mohammed, 1982; Aldridge *et al.*, 1993b). In the British and Siberian sections, elements of the *kentuckyensis* CBZ continue, whereas in the Norwegian section they do not. In the Norwegian and Siberian (Severnaya Zemlya) sections the appearance of *Pranognathus* can be correlated with the transgressive base of Global Cycle G2 (Männik, 1983; Worsley, 1989; Johnson *et al.*, 1991b). Therefore, this episode can be identified on Baltica, Avalonia and Siberia.

In low latitude Gondwana, the prioniodontid, *Pterospathodus cadiaensis* along with *Ozarkodina masurensis*, was recovered from the upper Baghdad Formation (Bischoff, 1986). The relationship between *Pterospathodus cadiaensis* and species of *Pranognathus* is not yet known (Männik & Aldridge, 1989), but the presence of a pterospathodontid at this point may indicate correlation with the *Pranognathus tenuis* Episode.

5.3.4 Low Diversity Episode

This episode can be identified on Avalonia (Britain) and Baltica (Oslo). The extinction/disappearance of *Pranognathus* occurred within the *Pentamerus* Beds of Britain (Avalonia) and when limestone became more dominant within the lower Ryatteraker Formation in the Oslo Graben (Baltica; Aldridge *et al.*, 1993b). Coniform

taxa recovered in Britain and the Oslo Graben include *Panderodus acostatus* and/or *Panderodus unicostatus*, *Panderodus panderi* and *Walliserodus* sp. Non-coniform taxa include *Pseudolonchodina fluegeli*, *Oulodus* sp. and *Distomodus staurognathoides* (Aldridge *et al.*, 1993b; Nakrem, 1983; Aldridge 1972, 1975).

In Britain (Avalonia), the overlying upper *Pentamerus* Beds and lower Hughley Shales Formation yield *Ozarkodina aldridgei*, *Ozarkodina excavata* and *Ozarkodina* aff. *O. oldhamensis*, and the coniform species *Decoriconus fragilis* and *Pseudooneotodus* sp. (Aldridge, 1972, 1985, Aldridge *et al.*, 1993b). The stepwise appearance of *Pseudooneotodus bicornis* and *Dapsilodus obliquicostatus* occurs through the lower Vik Formation (Nakrem, 1983). The appearance of *Dapsilodus* within this episode is also observed in the Anticosti Island section on Laurentia.

In New South Wales (low-latitude Gondwana), the Cadia Coach Shale Formation, which overlies strata bearing the first appearance of *Pterospathodus cadiaensis* is barren (Bischoff, 1986).

5.3.5 *Aulacognathus bullatus* Episode

The first appearance of *Aulacognathus bullatus* precedes that of *Pterospathodus celloni* in sections on Baltica and low-latitude Gondwana. On Baltica, the first appearance of *Aulacognathus bullatus* precedes that of *Pterospathodus celloni* by a number of meters within the Vik Formation (Aldridge *et al.*, 1993b), which has been interpreted as transgressive (Worsley, 1989; Johnson *et al.*, 1991b, fig. 3, 7, 8). Taxa that also first appear at this horizon include *Belodella silurica, Aulacognathus bullatus*, *Decoriconus fragilis Pseudooneotodus bicornis* (tri) and *Oulodus* sp. They all continue into the *celloni* CBZ, whilst *Dapsilodus obliquicostatus* disappears within this interval.

On low-latitude Gondwana (Australia), *Aulacognathus antiquus* and *Distomodus staurognathoides* appear within the basal Cobblers Creek Limestone Formation, which transgresses over the Panuara Hiatus (Bischoff, 1986). These sediments have been correlated with the *turriculatus* GBZ (Bischoff, 1986; Global Cycle G4). Other

taxa that occur in the strata below the first appearance of *Pterospathodus celloni* are species of *Aulacognathus* (*Aulacognathus angulatus*), *Pseudooneotodus* (*Pseudooneotodus* sp.), *Oulodus* (*Oulodus panuarensis*, *Oulodus australis*), *Oulodus planus planus* (=*Pseudolonchodina fluegeli*) and *Ozarkodina* (*Ozarkodina excavata eosilurica*, *Ozarkodina waugoolaensis*) (Bischoff, 1986). *Pterospathodus cadiaensis* reappears at the base of this formation, though only in one sample (Bischoff, 1986). *Distomodus* sp. A and *Aulacognathus bifurcatus* appear just below the first appearance of *Pterospathodus celloni* (Bischoff, 1986). On Laurentia this episode had only been identified within the Anticosti Island and Greenland sections. However, its occurrence within section in Baltica and Low-latitude Gondwana illustrates its global extent.

5.3.6 *Pterospathodus celloni* Episode

The base of the *celloni* CBZ and hence this episode, is a globally recognised event. It has been documented in Avalonia, Baltica and low-latitude Gondwana. The first appearance of *Pterospathodus celloni* occurs within the lower Hughley Shales Formation of Britain (Avalonia) and in the mid Vik Formation of Norway (Baltica; Nakrem, 1983). In Estonia, *Pterospathodus celloni* appears within the basal Velise Formation (Männik & Aldridge, 1989), which Johnson *et al.* (1991b, figs. 11-16) interpreted as transgressive (Global Cycle G4). On low-latitude Gondwana (Australia), the first appearance of *Pterospathodus celloni* occurs within the Glendalough Formation (Bischoff, 1986).

As on Laurentia, taxa that occur within the *celloni* CBZ in Avalonia, Baltica and low-latitude Gondwana include species of *Distomodus, Kockelella, Oulodus, Pseudolonchodina, Decoriconus, Panderodus, Walliserodus, Ozarkodina, Apsidognathus*, *Astropentagnathus, Aulacognathus* and *Icriodella* (Aldridge, 1972; Aldridge *et al.*, 1993b; Bischoff, 1986).

5.3.7 *Pterospathodus amorphognathoides* Episode

Examples of the *amorphognathoides* CBZ fauna have been recorded from Baltica (Oslo and Estonia; Aldridge & Mohammed, 1982; Männik & Aldridge, 1989) and low-latitude Gondwana (Australia; Bischoff, 1986). On Baltica, *Pterospathodus amorphognathoides* appears within the shallowing-upwards, Bruflat Formation and upper Vik Formation in the Oslo Graben section of Baltica (Aldridge & Mohammed, 1982; Worsley, 1989). Other taxa recovered include *Aulacognathus walmsleyi*, *Distomodus staurognathoides*, *Ozarkodina* aff. *O. gulletensis, Ozarkodina polinclinata*, *Pseudolonchodina fluegeli* and *Pseudooneotodus tricornis* (Aldridge & Mohammed, 1982)

On low-latitude Gondwana (Australia), the first appearance of *Pterospathodus amorphognathoides* occurs within the upper Glendalough Formation (*crenulata* GBZ), in strata which Johnson (1996) interpreted to represent a highstand (Global Cycle 5, herein). Species that first appear include *Oulodus planus borenorensis* (=*Pseudolonchodina capensis*), *Ozarkodina cadiaensis* and *Pseudooneotodus tricornis* (Bischoff, 1986).

5.3.8 Summary of pattern on other palaeocontinents

Each of the episodes have been identified on at least one other palaeocontinent and so the global nature of the episodes has been demonstrated. The goal of future research must be to sample more sections in different palaeocontinents, provinces and biofacies.

5.4 Discussion

5.4.1 Model of recovery

The appearance of two types of taxa can be observed within the recovery period in the Shelf and Slope Biofacies. These include taxa that evolved and remained within a specific biofacies (autochthonous taxa) and taxa that had evolved within one biofacies

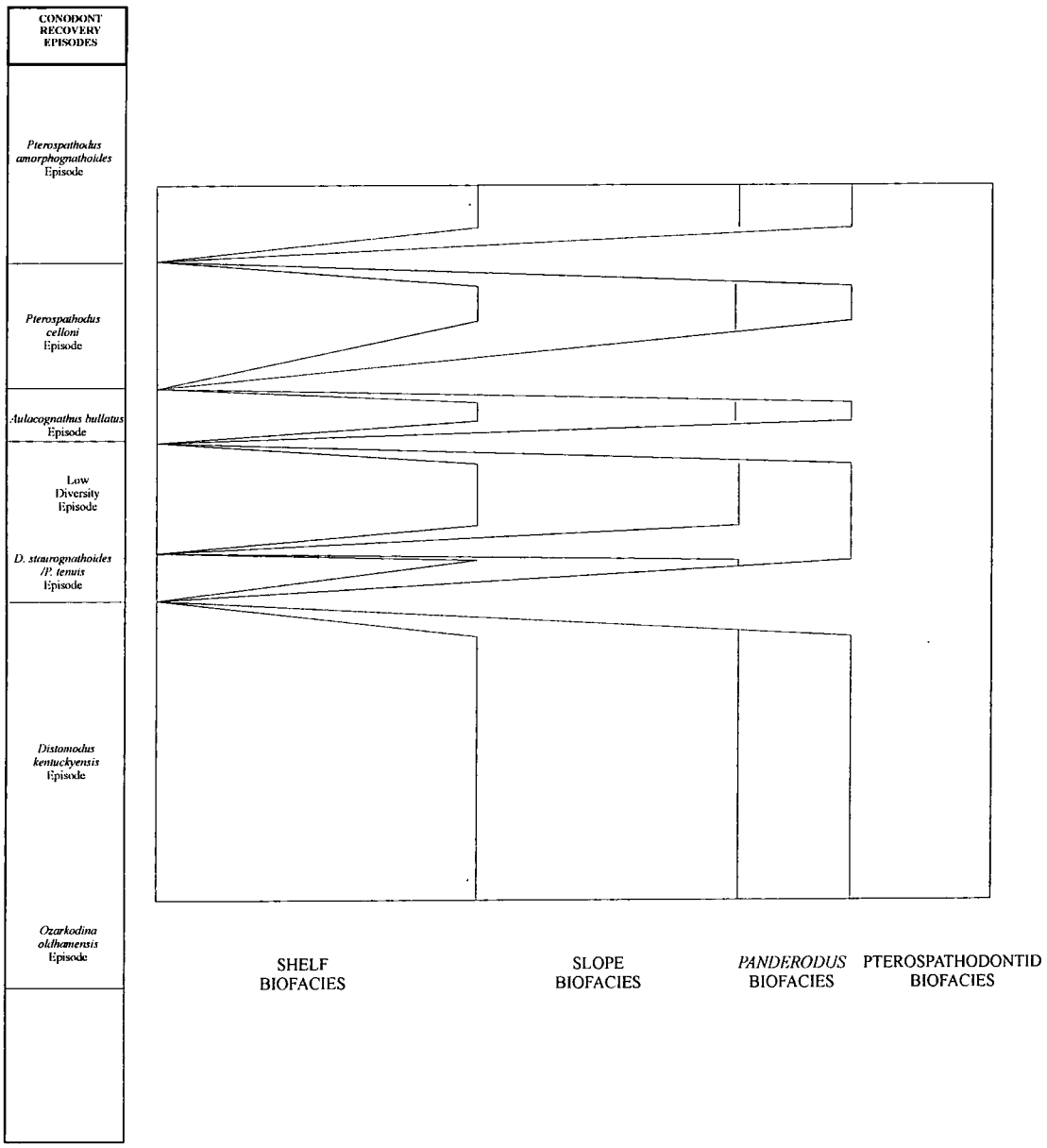


Figure 5.9 A schematic diagram depicting the migrations of elements of different biofacies through the Lower Silurian.

and migrated into others (allochthonous taxa).

The general pattern indicates that *in situ* (autochthonous) evolution occurred within each biofacies. For example, species of *Ozarkodina*, *Oulodus* and *Distomodus* evolved within the Shelf Biofacies, whilst species of *Pseudolonchodina* evolved within the Slope Biofacies. The appearance of new autochthonous taxa does not appear to have occurred at any one particular point within the sea-level cycles, but may have been linked to local changes in conditions.

Increases in diversity within the Shelf and Slope Biofacies appear to have occurred during the transgressive bases of Global Cycle G2, G4a, G4b and G5 (Figure 5.9). Taxa that appeared included species of *Pranognathus* and *Pterospathodus*. These taxa had not evolved within the Slope and Shelf Biofacies, but had migrated into those biofacies from somewhere else. This implies the occurrence of a Pterospathodontid Biofacies, whose location is yet unknown, possibly in very deep water or high latitudes (Figure 5.4; Section 5.4.2b). Elements of the Slope Biofacies (e.g. *Pseudolonchodina fluegeli*) also appeared in shelf areas dominated by the Shelf Biofacies during periods of transgression (Figure 5.9). Transgression drove taxa from the Pterospathodontid Biofacies into the Shelf and Slope Biofacies and elements of the Slope Biofacies into the Shelf Biofacies.

Exceptions to this pattern include the transgressive bases of Global Cycles G1 and G3. At the base of Global Cycle G1, the major post-glacial transgression, no representatives of the Pterospathodontids have been recovered. A possible reason for this being that the rootstock was much depleted following the end-Ordovician mass extinction event. Global Cycle G3 followed a severe sea-level fall, which has been associated with a positive $\delta^{13}C$ isotope excursion possibly indicating cooling (Wenzel, 1996; Heath *pers. comm.*). On Anticosti Island, the transgressive base of this cycle occurs within beds of the Richardson Member (Jupiter Formation), which have only yielded elements of *Panderodus*. During the subsequent regressive phase (Cybelé and Ferrum Members), taxa from the beds below began to reappear and were joined by *Dapsilodus obliquicostatus* and the brief reappearance of *Pranognathus*.

The occurrence of only *Panderodus* elements in the Anticosti Island section could indicate that the *Panderodus* Biofacies, suggested to occur in deeper water than the Slope Biofacies by Watkins & Kuglitsch (1997; Section 5.1.2), had moved on to the shelf during this episode. If this was the case, then the Slope Biofacies would be expected to appear in the section during the following regression. Supporting evidence for this is that *Dapsilodus obliquicostatus* appears for the first time in the Anticosti Island section during the regressive phase of Global Cycle G3. An alternative explanation is that local hostile environmental conditions, such as the formation of anoxic bottom waters and / or the impingement of the oxygen-minimum zone onto the shelf may have resulted in inhospitable conditions for most conodont species. Data from other sections is needed to resolve this discussion.

During the regressive phases of the sea-level cycles, biofacies shifted oceanward tracking the environmental conditions. Elements of the Slope Biofacies that had migrated into the Shelf Biofacies during transgression retreated back down slope. Pterospathodontids also disappeared from the Shelf and Slope Biofacies. They may have become extinct or retreated back to their primary habitat. It can be suggested that a rootstock must have remained in its primary habitat to fuel migrations during the following transgressions.

In summary, sea-level changes effected the recovery of conodonts during the uppermost Ordovician and Lower Silurian. Autochthonous taxa evolved within biofacies and the iterative appearance of allochthonous taxa within the Shelf and Slope Biofacies was triggered by transgressions.

5.4.2 The origins of Llandovery taxa.

In order to fully understand the recovery process, the ancestry of the Silurian-type taxa needs to be traced. The taxa that appeared during the initial recovery interval must have evolved prior to the extinction event, during the extinction event or have descended from survivors of the extinction event (Harries, 1995). They may have evolved *in situ* or migrated from other geographic areas or environments.

5.4.2a Initial Recovery Interval: Origin of Crisis Progenitor Taxa

Crisis Progenitor Taxa that appear within the Shelf Biofacies include species of *Ozarkodina*, *Icriodella*, *Distomodus*, *Kockelella* and *Oulodus*?. The evolutionary origins of *Icriodella* and *Distomodus* are discussed in Section 5.4.2b. The Genus *Oulodus* did occur within the Upper Ordovician and was common within the Shelf Biofacies. Late Ordovician and early Silurian species of *Oulodus* have been described as being so similar in morphology that they are likely to have evolved from the same stock (Sweet & Bergström, 1974; Sweet & Schönlaub 1975; Barnes & Bergström, 1988). In the Upper Ordovician species of *Oulodus* were common in the Shelf Biofacies and dominant in very shallow water (*Aphelognathus-Oulodus* Sub-biofacies of Sweet & Bergström, 1984) The Llandovery species *Oulodus*? *kentuckyensis* and *Oulodus*? *nathani* differ from species of *Oulodus* in the compression of the denticles. However, they have been suggested as related to *Oulodus* by McCracken & Barnes (1981).

The genus *Ozarkodina* had not been recorded from strata older than the Silurian, but Sweet & Bergström (1974) suggested that the Silurian species of *Ozarkodina* had evolved from Ordovician species of *Plectodina*. *Plectodina* was common within the Upper Ordovician Shelf Biofacies and was dominant in the mid-shelf within the *velicuspis* Chron (*Plectodina* Sub-biofacies; Sweet & Bergström, 1984). The genus *Kockelella* had also not been recorded from strata older than the Silurian. However, the Ordovician species *Ctenognathus pseudofissilis* Lindstöm has been suggested as the first known representative of the Kockelellidae, due to morphological similarities to *Kockelella* (Armstrong, 1990; Appendix A).

The main components of the Llandovery Slope Biofacies include *Pseudolonchodina*, *Dapsilodus*, *Decoriconus*, *Panderodus* and *Walliserodus*. They all had Ordovician representatives from which they are likely to have evolved, apart from the genus *Pseudolonchodina*, which first appeared within the Llandovery. There is a general similarity between the morphology of elements of *Pseudolonchodina* and *Oulodus*, but elements of *Pseudolonchodina* differ in being laterally compressed. The Genus *Periodon* also have morphological similarities to *Pseudolonchodina* and the elements of *Periodon* are laterally compressed. Thus, it has been suggested that an ancestral

link occurs between the two genera (Armstrong, *pers. comm.*). Species of *Periodon* were dominant within the Upper Ordovician Slope Biofacies, along with species of *Dapsilodus.* Therefore, the association of *Pseudolonchodina* and *Dapsilodus* within the Lower Silurian may suggest that the Llandovery Slope Biofacies was a direct continuation of the Upper Ordovician Slope Biofacies.

5.4.2b Origin of Prioniodontids

Prioniodontids that appeared within the Llandovery include *Icriodella*, *Distomodus*, *Pranognathus* and *Pterospathodus*. Species of *Distomodus*, *Pranognathus* and *Pterospathodus* had not been recorded in older strata than the Llandovery and so their ancestry is cryptic. Species attributed to the Genus *Icriodella* had been recorded from Ordovician sediments, but the Silurian and Ordovician species differed in morphology of the S elements and so a direct ancestral link was uncertain (Armstrong, *pers. comm.*)

Two main architectural and morphological categories of Prioniodontids have been recognised (Appendix A). *Icriodella* and *Distomodus* are representatives of Type I whilst *Pranognathus* and *Pterospathodus* are examples of Type II. In the Llandovery, the Type I Prioniodontids appear to have been more common in the Shelf Biofacies (e.g. *Icriodella*, *Distomodus*), whereas Type II Prioniodontids appear iteratively within the Shelf and Slope Biofacies (e.g. *Pranognathus* and *Pterospathodus*). Representatives of both types of Prioniodontids can also be observed within the Upper Ordovician strata. Representatives of Type I include *Gamachignathus* and *Birksfeldia,* whilst examples of Type II include *Amorphognathus* and *Promissium* (Appendix A). In the Upper Ordovician, *Gamachignathus* occurred on the margins of Laurentia within the Shelf Biofacies, whereas *Birksfeldia* has been reported from the Atlantic Faunal Region (Orchard, 1980; Appendix A). In the Upper Ordovician, *Promissium pulchrum* occurred at very high latitudes and has been recovered from the Soom Shale of South Africa, which overlies glacial tillites (Aldridge *et al.*, 1995), whilst *Amorphognathus* has been recovered from inner-shelf to slope sections (Bergström, 1983).

The similarity of apparatus structure and morphology of elements between the Ordovician and Silurian taxa indicates that the *Amorphognathus–Promissium* rootstock is likely to have given rise to the *Pranognathus-Pterospathodus* lineage. Likewise, the *Gamachignathus-Birksfeldia* rootstock was the likely origin for the Llandovery species of *Icriodella* and *Distomodus*.

The origination of the *Amorphognathus-Promissium* rootstock is thought to have occurred at high latitudes (Bergström, 1983). In the Upper Ordovician, *Promissium pulchrum* occurred at very high latitudes and has been recovered from the Soom Shale of South Africa, which overlies glacial tillites (Aldridge *et al.*, 1995). *Amorphognathus* is thought to have evolved on the high-latitude continent Baltoscandia during the Arenigian – Llanvirnian. It gradually expanded its geographic range during the Upper Ordovician, culminating in the essentially cosmopolitan distribution of *Amorphognathus ordovicicus* (Bergström, 1983). It has been suggested that the incursion of *Amorphognathus* into the Midcontinent Faunal Region during the Ordovician occurred during periods of transgression (see Fortey 1984). It is interesting to note that species of *Pranognathus* and *Pterospathodus* appear in shelf areas during periods of transgression through the Llandovery. This suggests that a rootstock of prioniodontids existed from the Upper Ordovician to Lower Silurian, and that elements of this stock were opportunists that expanded their ranges during periods of transgression.

5.4.2c The consequences for the origin of Llandovery biofacies

It has been established that a warm-water, Shelf Biofacies and a cool-water, Slope Biofacies existed during the Llandovery (Armstrong, 1990; McCracken, 1991b; Watkins & Kuglitsch, 1997). In addition a cooler water *Panderodus* Biofacies may have existed (e.g. Watkins & Kuglitsch, 1997), and the periodic appearance of pterospathodontid species in the Shelf and Slope Biofacies indicates that a fourth biofacies existed: a Pterospathodontid Biofacies. The location of the Pterospathodontid Biofacies is uncertain. Comparison with the *Amorphognathus-Promissium* rootstock would suggest that is was situated in high-latitudes or cooler water than the Slope Biofacies.

It can be seen from the discussion above that the main components of the Shelf Biofacies within the Lower Silurian evolved from Upper Ordovician taxa that had been abundant on the shelf. For example, the Ordovician genera *Plectodina* and *Oulodus* are thought to be the ancestors of the Silurian genera *Ozarkodina* and *Oulodus*. Likewise the main components of the Silurian Slope Biofacies are thought to have evolved from *Periodon* and *Dapsilodus*, which were dominant within the Upper Ordovician Slope Biofacies. This indicates that the hypotheses of Armstrong (1996) and Sweet & Bergström (1974), which state that the Silurian taxa were either all descended from the Ordovician Atlantic Faunal Region or all from the Midcontinent Faunal Region, are both too simplistic, as elements of the temperature related biofacies in the Lower Silurian seem to have evolved from their Upper Ordovician equivalents.

In general, major divisions can be seen at the family level between biofacies. Ozarkodininids occur within the Shelf Biofacies. Dapsilodontids and Prioniodontids occur within the Slope Biofacies. Prioniodontids occur within a separate deeper-water, Pterospathodontid Biofacies. Panderodontids and other coniforms occur within all biofacies, possibly blooming in the absence of other taxa.

5.4.3 The applicability of general recovery models.

The origination of new species during or following the extinction event has been suggested to have resulted from allopatric, sympatric or parapatric speciation (Charlesworth, 1990; Section 1.4.1). Differentiation between these three speciation mechanisms is difficult to ascertain from the fossil record. It can be suggested that during the glacial maximum, barriers would have been created between communities within the Shelf Biofacies, as a result of the falling sea level. This may have created geographically isolated communities within which genetic divergence occurred. Thus, allopatric speciation would have ensued. However, the fossil record is not complete enough for us to fully test this hypothesis.

The two general models for initial recovery of faunas following an extinction event have been discussed in Section 1.4. Jablonski (1986) suggested that survivors would

be limited to Ecological Generalists, whereas Kauffman & Harries (1996) suggested that a much more diverse rootstock would survive and enable rapid recovery (Harries *et al.*, 1996; Figure 1.2). Kauffman & Harries (1996) outlined the range of potential survivors involved in recovery, and mechanisms enabling their survival. The full range of taxa that they identified included: Ecological Generalists, Disaster Species, Ecological Opportunists, Pre-adapted Survivors, Crisis Progenitor Taxa, Stranded Populations, Short-Term Refugia Species and Long-Term Refugia Species (see definitions in Section 1.8).

A number of the taxa defined by Kauffman & Harries (1996) can be identified in the recovery record of conodonts following the end-Ordovician extinction event (Figure 5.10). For example, a number of taxa that can be described as Ecological Generalists survived the extinction events. These include *Decoriconus costulatus*, *Pseudooneotodus beckmanni* and species of *Panderodus*. They are the only species to survive the extinction events unaltered.

A number of Silurian-type taxa that appeared between the two extinction events may be referred to as Crisis Progenitor Taxa, due to the fact that they appear during the glacial maximum (a time of crisis). Examples of Crisis Progenitor Taxa include *Ozarkodina oldhamensis*, *Ozarkodina hassi*, *Oulodus*? *nathani*, *Oulodus*? *kentuckyensis* and *Kockelella manitoulinensis*. Kauffman & Harries (1996) predicted that these taxa (Crisis Progenitor Taxa) would fuel radiation following an extinction event. However, they did not fuel a major radiation in the uppermost Ordovician to Lower Silurian. The taxa that appeared during or immediately prior to the extinction events continued through the Rhuddanian and Lower Aeronian, and only a small number of new species appeared during that period.

The fossil record of conodonts through the uppermost Ordovician and Lower Silurian indicates that survivors of the extinction event were limited to the Crisis Progenitor Taxa and Ecological Generalists. However, the iterative appearance of pterospathodontids within the Aeronian and Telychian indicates that other survivors, that are not recorded in the uppermost Ordovician and basal Silurian, must also have survived. They can be described as Long-Term Refugia Taxa, and examples include *Pranognathus tenuis* and *Pterospathodus celloni*.

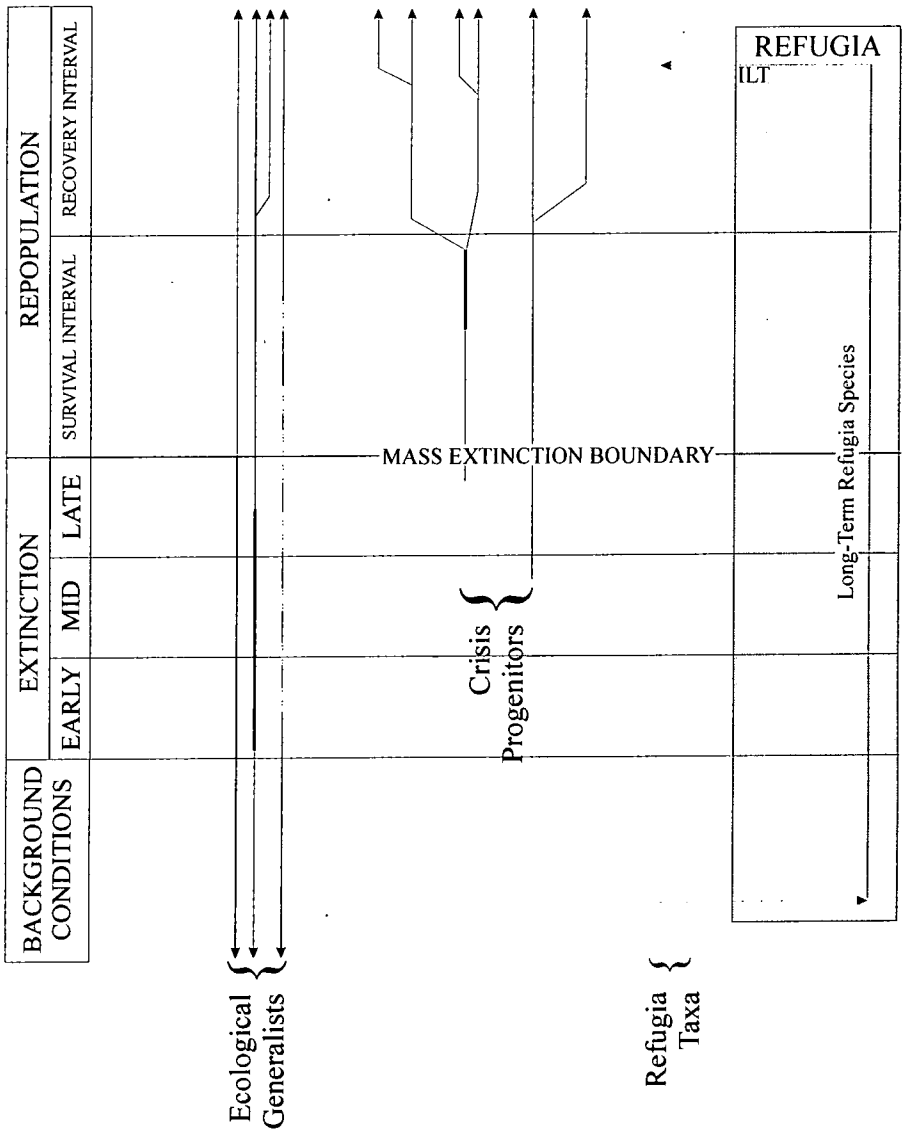


Figure 5.10 The Model of survival and recovery from Kauffman & Harries (1996) applied to the recovery of conodonts following the end-Ordovician mass extinction event. For term definitions, refer to Section 1.8. For key refer to Figure 5.3

Examples of Ecological Generalists, Crisis Progenitor Taxa and Long-Term Refugia Taxa have been identified in the record of conodont recovery following the end-Ordovician mass extinction event (Figure 5.10). Thus, the suggestion by Jablonski (1986) that survivors of mass extinction events would be limited to Ecological Generalists is not supported herein. However, evidence of the other taxa described by Kauffman & Harries (1996), such as Opportunistic Taxa, Disaster Taxa, Stranded Populations and Short-Term Refugia Taxa has not been identified. Thus, the terminology created by Kauffman & Harries (1996) is only partially applicable to the recovery of conodonts following the end-Ordovician mass extinction event.

It has been discussed above that a model specifically detailing long-term recovery has not yet been developed. The long-term recovery of species may be described in terms of macroevolutionary theories, which include the Punctuated Equilibrium Model (Gould & Eldredge, 1993), *Plus ça change* Model (Sheldon, 1996) and the Red Queen Model (Section 1.4.2). The pattern of long-term recovery has been summarised above (Section 5.4.1). Evolution occurred within each biofacies and was interrupted by iterative migrations of taxa from other biofacies. In the Slope Biofacies at Prongs Creek, the gradual evolution of *Pseudolonchodina capensis* from *Pseudolonchodina fluegeli* can be observed. Elements that could be assigned to *Pseudolonchodina capensis* were recovered within samples yielding *Pseudolonchodina fluegeli* well before the appearance of *Pseudolonchodina capensis*. Thus, evolution within the Slope Biofacies may have been predominantly gradualistic.

Within the Shelf Biofacies many species of *Ozarkodina* appeared. However, the gradual evolution of one species in to another has not been observed. This may be an artifact of the lack of a continuous fossil record, or it may indicate that evolution was not gradually occurring within the Shelf Biofacies, and that new species evolved during steps possibly triggered by an environmental change.

The evidence would suggest that gradual evolution may have occurred within the Slope Biofacies whilst punctuated evolution occurred within the Shelf Biofacies. The evolutionary pattern occurring within the Pterospathodontid Biofacies is uncertain. The gradual evolution of *Pterospathodus celloni* to *Pterospathodus*

amorphognathoides in an Estonian borehole described by Männik & Aldridge (1989) suggests that the pattern of evolution was gradual within this biofacies. Thus, the pattern of evolution appears to have differed between different biofacies / environments. This is predicted by the *Plus ça change* Model of Sheldon (1996), which suggests that punctuated equilibrium will occur in widely fluctuating physical environments (e.g. shallow water), and in more stable environments (e.g. deepwater) continuous gradualistic evolution would dominate.

5.4.4 The mechanisms hindering and driving recovery.

It has been illustrated that changes in sea level affected the recovery of conodonts, but the driving force of the sea-level cycles is uncertain. There are eight transgressive-regressive cycles within the Llandovery of varying length (this include the Laurentian cycles within Global cycle G1). The duration of the Llandovery has been estimated at 13 Ma (Hughes, 1995) suggesting an average cycle length of 1.6 Ma.

The causes of relative sea-level change have been discussed by Donovan & Jones (1979). Climatic causes include the thermal expansion and contraction of the water column due to warming or cooling (Donovan & Jones, 1979). Fluctuations in sea level may also result from the differences in the amount of water stored on land during glacial and non-glacial episodes (Jacobs & Sahagian, 1993). Other mechanisms include orbital forcing, such as Milankovitch cyclicity (for a review see De Boer & Smith, 1994), or tectonic mechanisms, such as variations in mid-ocean ridge activity (Hays & Pitman, 1973) and intra-plate stresses (Cloetingh, 1988).

It has been discussed in Chapter 2 that glacial deposits accumulated during four periods within the Llandovery and that the sea-level cycles within the Llandovery were related to waxing and waning of the ice sheets (Johnson, 1996). However, the dating of the glacial deposits is not yet precise enough to enable exact correlation with the sea-level cycles (Section 2.7.1). The correlation of a positive $\delta^{13}C$ isotope excursion and a sea-level fall within the *sedgwickii* GBZ may indicate that it is cooling / glacial conditions that caused the sea-level falls (Wenzel, 1996; Heath *pers.*

comm.). However, isotope excursions are not found at other times within the Llandovery, perhaps suggesting that the cooling episodes varied in magnitude.

The periodicity of the cycles may reflect Milankovitch cyclicity. However the sea-level cycles are longer (1.6 Ma) than those usually attributed to Milankovich cycles (De Boer & Smith, 1994). However, shorter cycles may have occurred within these long-term cycles. In the Anticosti Island section, Long (1996) identified 4 transgressive-regressive cycles within the Becscie Formation (Laurentian Cycle L1a). If Laurentian Cycle G1a has a duration of 1.6 Ma, this would indicate that the smaller scale cycles had a duration of 400,000, which is of comparable duration to an eccentricity cycle (De Boer & Smith, 1994). Therefore, the long-term cycles identified may in fact by caused by Milankovitch cyclicity or perhaps a combination of Milankovitch cycles and tectonic mechanisms, as the Iapetus Ocean was closing at this time.

The current data are inconclusive regarding the driving forces of these events. The most attractive mechanism is Milankovitch cyclicity. Even though the driving mechanism is not yet fully understood, it has been conclusively illustrated that the recovery of conodonts following the end-Ordovician mass extinction event was related to climate change.

5.4 Conclusions

- Recovery occurred in a stepwise pattern following the end-Ordovician mass extinction event.
- Initial recovery was fuelled by the appearance of Crisis Progenitor Taxa during the glacial maximum to initial post-glacial period.
- Continued recovery was linked to climatic changes through the recovery interval. Iterative migrations of allochthonous taxa in to the Shelf and Slope Biofacies occurred during transgressions.
- A low diversity episode occurred within the Aeronian, which followed a cooling episode.

- The iterative appearance of Pterospathodontids suggests the presence of a Pterospathodontid Biofacies in cooler water than the Slope Biofacies.
- Taxa characteristic of the Llandovery Shelf and Slope Biofacies appear to have evolved from taxa within the Upper Ordovician Shelf and Slope Biofacies, respectively.
- The Kauffman & Harries (1996) model can be partially applied to the pattern of conodont recovery. Ecological Generalists, Crisis Progenitor Taxa and Long-Term Refugia Taxa can be identified within the record of conodont recovery.
- The long-term recovery pattern supports the *Plus ça change* Model of Sheldon (1996), which suggests that the pattern of recovery would vary in different environments.
- The recovery of conodonts in the Lower Silurian was climatically driven.
- The recovery was linked to sea-level cycles, which may be orbitally driven.
- Improving sampling resolution and increasing the number of localities sampled through the Llandovery must be a priority for future studies.

Chapter 6

Conclusions

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6.1 Conclusions

The end-Ordovician mass extinction dramatically altered the course of conodont evolution. This extinction event is probably unique in that it can be strongly correlated with a glacial climatic control. This study has identified, through the application of high-resolution stratigraphy, events within the extinction and recovery intervals.

Elements of the uppermost Ordovician Shelf-edge Biofacies were severely affected by the oceanic cooling and introduction of cold-water currents associated with the initiation of the glacial maximum. In contrast, elements of the Shelf Biofacies were more severely affected by the intense cooling, shallowing and overcrowding during the glacial maximum. A number of the Shelf-edge taxa that had survived the glacial maximum suffered extinction at the hands of increasing water temperatures, rising anoxia and/or the cessation of oceanic circulation during the post-glacial transgression.

Recovery was initiated by the appearance of Crisis Progenitor Taxa within the glacial maximum in the Shelf Biofacies and during the post-glacial transgression in the Shelf-edge–Slope biofacies. The Shelf-edge Biofacies identified within the uppermost Ordovician is not recognised in the Lower Silurian. Two main biofacies occurred on the Shelf and Slope, which had directly evolved from their Upper Ordovician equivalents.

The long-term recovery involved the evolution of Crisis Progenitor Taxa and Ecological Generalists within the Shelf and Slope Biofacies (autochthonous taxa). Punctuated equilibrium likely predominated in the Shelf Biofacies as a consequence

of widely fluctuating physical conditions. In contrast, the more stable environments of the slope encouraged gradualistic evolution within the Slope Biofacies (*Plus ça change* Model).

Transgressive episodes within the Llandovery, possibly linked to eccentricity cycles, caused the iterative appearance of Long-term Refugia Taxa (allochthonous taxa), sourced from a Pterospathodontid Biofacies. The transgressive episodes also drove elements of the Slope Biofacies onto the shelf.

It has been observed that the mechanisms driving extinction, namely environmental disruption and temperature changes, were also responsible for fuelling the subsequent recovery.

6.2 Summary of Conclusions

- The pattern of conodont extinction in the uppermost Ordovician varies in different palaeoenvironments.
- In shelf-edge and slope sections, conodonts suffered extinction within the upper *pacificus* to *extraordinarius* GBZs, associated with the onset of the glacial maximum, and during the post-glacial transgression.
- In inner- and mid-shelf sections conodonts were not severely affected by the initiation of the glacial maximum, but became extinct within the glacial maximum to post-glacial period.
- Extinctions were caused by the changes in sea-level temperature, habitat space and oceanic circulation associated with the initiation, intensification and cessation of the glacial maximum.
- Recovery occurred in a stepwise pattern following the end-Ordovician mass extinction event.
- Initial recovery was fuelled by the appearance of Crisis Progenitor Taxa during the glacial maximum to initial post-glacial period.
- Continued recovery was linked to climatic changes through the recovery interval. Iterative migrations of allochthonous taxa into the Shelf and Slope Biofacies occurred during transgressions.

- A low diversity episode occurred within the Aeronian, which followed a period of cooling.
- The iterative appearance of Pterospathodontids suggests the presence of a Pterospathodontid Biofacies in cooler water than the Slope Biofacies.
- Taxa characteristic of the Llandovery Shelf and Slope Biofacies appear to have evolved from taxa within the Upper Ordovician Shelf and Slope Biofacies, respectively.
- The Kauffman & Harries (1996) model can be partially applied to the pattern of conodont recovery. Ecological Generalists, Crisis Progenitor Taxa and Long-Term Refugia Taxa can be identified within the record of conodont recovery.
- The long-term recovery pattern supports the *Plus ça change* Model of Sheldon (1996), which suggests that the pattern of recovery would vary in different environments.
- The recovery of conodonts in the Lower Silurian was climatically driven.
- The recovery was linked to sea-level cycles, which may be orbitally driven.
- Improving sampling resolution and increasing the number of localities sampled through the Llandovery must be a priority for future studies.

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